

THE FRANCOLINS,
A STUDY IN SPECIATION

BY

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INTRODUCTION

Thirty-nine species of francolin (*Francolinus* and *Pternistis*) were recognised in Peters' Check List of the Birds of the World 2, 1934, of which thirty-four are African and five Asiatic: one (*F. ochropectus* Dorst & Jouanin, 1952) has been described since. I have rearranged Peters' species slightly, now recognising thirty-six in Africa and five in Asia. As is inevitable a Check List employing conventional nomenclature gives no indication of the relationship between the species which must be the basis for any discussion on speciation. The objectives of this paper are therefore twofold: firstly to set out in the text and on the maps the present relationship between the species. This is not as formidable a task as might be expected

from the number of species involved, for thirty-seven of the forty-one fall readily into eight groups, seven of which are African and one Asiatic. (In this paper the term "group" is used for either a superspecies, in which all members are largely allopatric, or for a species group which is a rather looser assemblage of related forms containing some species which are partly sympatric with other members.) These groups are discussed and mapped separately with particular reference to their ecology and the relationship of neighbouring or sympatric forms. The four species that do not fall readily into any group are discussed separately at the end.

Secondly, from the pattern presented by the birds of each group and by their distribution I have tried to reconstruct the climatic changes, with the resultant isolating and rejoining of populations, which could have formed this pattern. In doing so I am fully conscious that the picture we see today gives only fragmentary clues to the past and that it is impossible to interpret accurately any but the simplest situations. Nevertheless, even in the most complex groups, I believe there is some usefulness in making the attempt, for if a series of studies of this nature suggests changes that from other branches of science are known to have occurred, it may be possible to give some tentative datings to various steps in speciation.

Throughout the preparation of this paper I have been particularly fortunate in being able to discuss the problems with R. E. Moreau, who has been preparing concurrently a paper on "The Vicissitudes of the African Biota in the Late Pleistocene". He has allowed me to quote as Appendix 1 a summary of his conclusions of the major climatic changes that have taken place in Africa in the past 60,000 years. In acknowledging my gratitude to him for this and for invaluable advice and criticism I must also absolve him from any responsibility for some of my interpretations of the evolutionary stages, or the conclusions which I have drawn from them.

I am also deeply indebted to M. P. Stuart Irwin who prepared distribution maps for me of all the francolins in the National Museum of Southern Rhodesia: also to Dr. H. Friedmann, C. W. Benson and I. C. J. Galbraith for criticism of the manuscript. Others to whom I am grateful for loans of specimens, advice, or other help, include Dr. Dean Amadon, Professor J. Berlioz, P. Blasdale, Mgr. F. O. Cave, E. M. Cawkell, Dr. James Chapin, P. A. Clancey, Miss M. Courtenay-Latimer, I. H. Dillingham, H. J. de S. Disney, Sir Hugh Elliot, W. V. Harris, M. J. Hollis, Cdr. A. M. Hughes (who drew figure 1), Gen. Sir Gerald Lathbury, C. W. Mackworth-Praed, Miles Markus, Col. R. Meinertzhagen, Captain C. R. S. Pitman, O. P. M. Prozesky, Professor H. Schouteden, Rev. Dr. W. Serle, R. H. N. Smithers, B. W. H. Stronach, M. A. Traylor, Dr. C. Vaurie, Col. Jack Vincent, Professor V. Van Straelen, John Williams, Dr. J. M. Winterbottom.

THE GENUS

The francolins are recognised as a branch of the sub-family Phasianinae (Partridges, Quails, Pheasants) which comprises over fifty genera, most of which are Palaearctic or Asiatic. My interest for this paper is primarily in the African members of the genus, but the five Asiatic species are included since they provide

some interesting points of comparison. I am not, however, competent to enter into a discussion on the limitations of the genus in Asia where there are thirty-eight other genera in the same sub-family some of which such as *Rhizothera*, *Alectoris*, *Perdix*, *Arboricola* seem closely related to *Francolinus*. They have been distinguished on various structural characters such as the number of tail-feathers, the size and shape of the bill, or the length of tail, and I have accepted these distinctions uncritically. It is sufficient to say that the francolins are characterised by a rather longer, more hooked bill than members of the other genera (except *Rhizothera*), a short tail of fourteen feathers, and an upright stance: in the majority of species the male, at least, is spurred. The range of colours in the plumage is limited to the shades of ochre, chestnut, brown, black and white produced by melanic pigments, but the pattern of individual feathers is complex and varied.

The partridge of Madagascar, *Margaroperdix*, has also some similarity to the francolins (particularly to the forest francolin *F. lathamii*) in colour and pattern, but has various structural differences in bill, tail and legs, which make it doubtful if the two are very closely related. Apart from this in the Ethiopian region there are no gamebirds that can be regarded as similar to francolins in either structure or habits, the only others being the quails (*Coturnix* and *Excalfactoria*), the Stone Partridge (*Ptilopachus*)—a bird confined to the savanna and steppe belt north of the Equator—the Congo Peacock (*Afropavo*), confined to the Congo forest, and the guinea-fowl family (Numididae).

I would suggest therefore that the closer affinities of *Francolinus* with Palaearctic and Asiatic genera indicate that it originated in Asia, becoming separated from the other game-birds as a species particularly adapted to sub-tropical grasslands, and that later it spread into southern Europe and Africa. Once in Africa lack of efficient competition allowed it to spread widely and to exploit varied habitats which, in Asia, are occupied by other related genera.

If this hypothesis of the origin of *Francolinus* is accepted it is apparent that there are factors present in Africa that have encouraged speciation in the comparatively recent past (since the emergence of the genus). This is readily acceptable in view of the climatic changes known to have taken place (see Appendix 1). Fluctuations in humidity and temperature would cause redistribution of the montane and lowland forests, and the woodlands, savannas and steppes, isolating and rejoining the populations of their indigenous birds.

Among the francolins various generic divisions have been proposed, the most commonly accepted being *Pternistis* for the bare-throated francolins (as in Peters', 1934: 84). However, I agree with White (1952) that the bare throat alone is not a generic character and in other respects these birds are closer to some of the other large francolins than are other members of the genus. If a generic division was to be made I would separate the birds of the first five groups (including the Bare-Throated Group) which have relatively plain or vermiculated backs, from the birds of the last three groups with striated or quail-type patterning on the backs, placing *F. gularis* with the former and *F. pondicerianus* and *F. lathamii* with the latter. However, I regard such a division as unnecessary and leading to difficulties in respect of the rather atypical species *F. nahani*.

For a study on speciation francolins have the advantage of being remarkably sedentary birds for their size, not disposed to fly any great distances, and closely associated with a particular habitat. Morphologically the bold colours and patterns, particularly on the underparts, have the advantage of indicating where interbreeding has or has not taken place between neighbouring forms. Finally their "sporting" and edible qualities have given them an interest to many people other than ornithologists so that their ranges and habits are probably rather better known than those of any comparable group: at the same time these qualities have led to a persecution of the genus over the last fifty years which, combined with the damage done by intensive agriculture to the natural habitats, has almost exterminated species from some areas in which they were common and renders it difficult, if not impossible, to get further information about the habits of species from some areas which are now "developed".

THE GROUPS

Grouping the francolins has presented little difficulty, for the close relationship of most members is evident from their appearance, ecology and distribution and has been recognised by previous authors. In a few cases where the relationship is less obvious this is discussed in the text. I have felt that it facilitates discussion to give descriptive names to the groups rather than numbers, and the names chosen indicate an important character common to all members though it has not been possible in all cases to find a character which is exclusive to the group.

The order in which the groups are listed and discussed is not intended to be systematic except that the first five and the last three appear to form related assemblages.

The groups and the species that comprise them are as follows:—

1. Spotted Group (*francolinus*, *pictus*, *pintadeanus*).
2. Bare-throated Group (*afer*, *swainsonii*, *rufopictus*, *leucoscepus*).
3. Montane Group (*erckelii*, *ochropectus*, *castaneicollis*, *jacksoni*, *nobilis*, *camerunensis*, *swierstrai*).
4. Scaly Group (*ahantensis*, *squamatus*, *griseostriatus*).
5. Vermiculated Group (*bicalcaratus*, *icterorhynchus*, *clappertoni*, *hildebrandti natalensis*, *hartlaubi*, *harwoodi*, *adpersus*, *capensis*).
6. Striated Group (*sephaena*, *streptophorus*).
7. Red-winged Group (*psilolaemus*, *shelleyi*, *africanus*, *levaillantoides*, *levaillantii*, *finschi*).
8. Red-tailed Group (*coqui*, *albogularis*, *schlegelii*).

The four species not assigned to any group are the two African forest francolins *lathamii* and *nahani*, and the two Asiatic species *pondicerianus* and *gularis*.

SPECIES AND SUBSPECIES

In discussing speciation it must always be borne in mind that this is a continuous divergent progress starting when two populations become isolated from each other. In isolation each will develop divergent characters, either morphological or ecological, or both, but there will be a long period during which the two populations are

sufficiently alike for free interbreeding to take place if the isolating barrier is removed (Phase 1). If they remain isolated and divergence continues this stage will gradually merge into one in which the divergent characters become such that interbreeding is unlikely (but not impossible) if the two populations rejoin (Phase 2). Again these characters may be ethological, involving different recognition patterns or voice; or ecological, so that the two are unlikely to occur on the same ground; or could possibly be a difference in breeding seasons. It is in this stage that the occasional hybrid may be produced in the wild, and in which hybridisation is possible and frequent under artificial conditions. Finally the two birds diverge so completely that they are incapable of interbreeding (Phase 3).

In general most populations in Phase 1 and in the transition period between Phase 1 and 2 would be regarded as subspecies and those in Phase 2 and 3 as species, but there is no line between them and the decision must rest on the assessment of the taxonomist. This must be based on the degree of divergence and the degree to which they are known to interbreed. In the francolins members of different groups may be assumed to have reached, or almost reached, Phase 3 in their relationship, but the allopatric members of each group may be only in Phases 1 and 2.

Each group provides a case in which I have had to make an arbitrary decision whether or not to regard neighbouring forms as conspecific. For example, in the Spotted Group *F. francolinus* and *F. pictus* have diverged appreciably, especially in males, and hybrids are scarce, so I treat them as species. In the Bare-throated Group the *afer* block and the *cranchii* block have also diverged but interbreed freely, so are treated as conspecific. In the Montane Group *F. ochropectus* has diverged morphologically and ecologically from *F. erckelii* and is isolated, so is treated as a species, while *atrifrons* stands in a similar morphological relationship to *castaneicollis* but has the same field habits so is considered conspecific. In the Scaly Group the Niger provides a barrier between *F. ahantensis* and *F. squamatus* so it is not certain if they are capable of interbreeding but they seem to have diverged sufficiently to justify specific status. In the Vermiculated Group *F. hildebrandti* and *F. natalensis* have diverged, especially in the females, but interbreed to a limited extent at one point of contact but not apparently at another so are treated as species. In the Striated Group "rovuma" type birds (with a streaked abdomen) apparently do not interbreed with "sephaena" types (unstreaked) in the southern half of the range but hybridise in the north; the divergence is slight, however, and they are treated as conspecific. In the Red-winged Group the degree of divergence and the relationship between *shelleyi* and its three neighbours, *africanus*, *whytei*, and *uluensis* varies only slightly, but is just sufficient for me to treat *africanus* as a species and the other three as conspecific. In the Red-tailed Group the northern forms of *coqui* have diverged slightly, both morphologically and ecologically, from the southern but seem capable of interbreeding so must be considered conspecific.

The foregoing demonstrates the impossibility of defining a species in such conditions. For this reason I have tried to avoid differentiating strongly between species and subspecies in the discussion, though greater clarity might have been achieved by setting out the discussion under specific headings (as has been done in the Red-winged Group where rearrangement of the species made it necessary).

On the other hand I have endeavoured to make a clear distinction between those subspecies which I term "potential species"—namely those which are either (a) isolated at present, or (b) must be assumed to have been isolated at some period, since they show a degree of divergence from their neighbours which is too great to be attributable to local ecological factors—and those subspecies whose divergence can be attributed to ecological factors and which, as a rule, form part of a cline. The characters and ranges of "potential species" are defined equally with those of full species, but other subspecies are noted summarily in smaller print in a section in each group headed "Other variation", together with any significant local or individual variation. On the maps as much information as possible has been shown on the ranges and relationships of species and subspecies, but this has necessarily been dependent on the complexity of each map. However, I do not consider it practical or desirable to recognise numerous steps in a cline, or slight local variations, and have relegated to the synonymy many names given to such intermediates and micro-populations. There is more justification in naming isolated populations, however small, such as some of the montane ones, and in these cases I have been guided by the degree of divergence shown. For instance, I regard names as desirable for such highly divergent small populations as the montane francolins found on the Plateau du Day in (French) Somaliland (*ochropectus*) and at Mega in southern Abyssinia (*atrifrons*), but not for others in the same group in other mountains of southern Abyssinia which differ only slightly from each other. To avoid encumbering the main discussion with irrelevant detail, notes on taxonomy and synonymy are confined to an appendix.

In the parts of the paper dealing with evolution the ancestral stock of present species or of more than one species is referred to with the prefix "proto" (e.g. *proto-coqui* and *proto-albogularis/schlegelii*): if clarity demands, the name is followed by "subsp." or "sp.". The name of the author and date of publication are inserted only for those subspecies not listed by Peters (1934).

METHODS

The extensive collection of francolins in the British Museum has formed the basis for this study, supplemented by loans of critical specimens from other museums. All the African specimens examined and all the authentic records I have been able to trace in literature have been plotted over the Vegetation Map of Africa (Oxford 1959), as many species as possible being entered on a single sheet. This has enabled me to make a direct comparison of the range of any species with the vegetational belts and with the range of other species, whether in the same group or not. The Asiatic species have been plotted with accuracy only in the few critical areas, and for this the distribution maps of Indian birds prepared by Whistler, but never published, have been of great assistance. The maps of the groups have been compiled from these key maps. In a distribution map it is always difficult to know to what extent the range should be shown as continuous between actual collecting points, and in this respect the maps differ. For the Asiatic species I have shown the

limits of the range only: for the African species I have, as a general rule, shaded only areas from which specimens have been obtained, though this may give a rather distorted picture from parts of the country which are least known ornithologically: in a few cases, most notably for the Bare-throated Francolins (Map 2), I have felt that greater clarity in presentation could be achieved by shading the whole area within the limits of the range: this has been done only with species which, from their known habitat preferences, could be expected to have a reasonably continuous distribution within a vegetation belt.

The morphological discussion is based on specimens examined personally unless otherwise stated. For the field notes I have used the standard regional works as a basis but these have been immeasurably enriched by the numerous conversations and letters that I have exchanged with the many field workers whose names appear in the acknowledgments. Where these workers have been responsible for specialised information I have tried to give the credit in the text, but they are responsible also for much of the general information which is incorporated without acknowledgment.

I have found it difficult when discussing ecology and habitat to be consistent in the descriptive terms used, especially in correlating the parts of southern Africa with which I am familiar with those of the north for which I have to rely on the descriptions of others. As far as possible I have followed the terminology employed by the Vegetation Map of Africa (Map 11). In this the vegetational types which mainly concern the francolins are the Woodlands, Savannas and Steppes (Types 16-25). My own experience in southern Africa and the works of such specialists in ecology as Benson and Stuart Irwin show the importance of the distinction between the woodlands in which acacia is rare or absent (the "brachystegia woodlands" or "myombo"—Types 18 and 19) and the acacia country, whether it is termed acacia "woodland", "savanna" or "steppe". This distinction applies not only to the birds of the actual woodlands but also to those of the grasslands and savannas (i.e. grasslands with scattered trees) with which the woods are interspersed, many birds being strictly confined to either the brachystegia belt or to acacia. (In the southern and eastern francolins there are, in fact, several species indigenous to acacia, such as *F. sephaena*, *F. leucoscepus*, *F. rufopictus*, *F. adspersus* and *F. levaillantoides*, but none which is wholly indigenous to the woodland belt, though the potential species *F. s. shelleyi* and *F. s. whytei* and the Bare-throated *F. afer* nearly qualify.) I have therefore made a clear distinction in the discussions between the brachystegia belt and acacia country and throughout the paper the term "woodland" is used exclusively for types 17-19 unless "acacia woodland" is specifically stated.

North of the equatorial forest the woodlands are apparently similar in character to the brachystegia woodlands though composed largely of different species of trees and less continuous (Type 17). I am told also that, because of this discontinuity, the transition from the woodland belt to the acacia is less clearly defined. It is to be expected that there are therefore less clear-cut ecological distinctions in the birds, but this is not easy to determine from published works, the term "savanna" being widely used by different authors without clear definition. I have therefore been less precise in discussing the habitat of northern francolins. (From the maps it

appears that *F. clappertoni* and *F. coqui spinetorum* may be indigenous to acacia, and *F. schlegelii*, *F. albogularis* and *F. icterorhynchus* to the woodland belt.)

The distinction between acacia "woodlands", "savannas" and "steppes" is largely one of aridity and the transition between the types is necessarily gradual. It will be appreciated from the foregoing that savannas are found in both the woodland and acacia belts, but they are necessarily different in character. Where the term is used without qualification it should be plain from the context which belt is under discussion.

In attempting to interpret in terms of evolution the pattern presented in each group by divergence, ecology and ranges, I have started in each case with the distributional maps. From these I have tried to find in each group the factor that limits the ranges. More often than not the answer lies in the vegetation map, and the range of a group, species or potential species will be found to coincide with the limits of a vegetation belt, this coincidence being particularly common where acacia savanna or steppe changes to woodland. The presence or absence of mountains, hills or rivers is obviously significant in other cases, but here it must be remembered that, while the reason for the present discontinuity in the range of a species may be self-evident, the range must have been continuous in the comparatively recent past. In one case, the Red-winged Group, the limits of ranges of species coincide not so much with the vegetational belts as with the isohyets of total annual rainfall. In another, the Striated Group, the isolated areas from which one species (*F. streptophorus*) is found seem to have nothing in common except that they are the two ends of a ridge of higher country. In several cases where there seems no ecological reason for the limits of a species' range the bird is replaced by a member of another group. From facts such as these I have tried to assess in what conditions each group would be most likely to thrive at the expense of other groups, and, conversely, what conditions would be sufficiently unfavourable to divide it into isolated populations from which the species developed. In postulating in each group successive climatic changes to account for the isolating and rejoining of the various populations I have been guided solely by the pattern presented by the birds themselves, and not by any consideration of what climatic changes are known from other evidence to have occurred, except that I have not, I hope, postulated any changes which are, on this evidence, outside the bounds of possibility. However, in the final section of the paper I have tentatively tried to correlate some of the climatic eras postulated with those known, as listed in Appendix 1.

In the discussion on evolution two assumptions are frequently made which are not necessarily correct but which seem sufficiently probable to justify their use as a basis for hypothesis. The first is the premise that the degree of divergence shown by two isolated forms can be correlated with the length of isolation. This, of course, is not necessarily true, but it can, I think, be accepted that in similar circumstance there is a likelihood that speciation will proceed at approximately the same pace; also that a comparatively long interval must elapse for considerable divergence to take place in isolates. The corollary premise that isolates that have not diverged extensively have not been long separated is more open to doubt, and examples (such as the forest owl *Phodilus prigoginei*) can be quoted of populations that must

have been long isolated but show little divergence. But I regard these as exceptional.

The second assumption is that the present species and potential species originated in some part or parts of their present range. This is a premise that is the more questionable in the case of species which are not members of superspecies. However, in the francolins these are exceptional, most of the species being part of a superspecies in which all members are allopatric and which has a more or less continuous distribution over a large part of Africa. In these cases it is highly improbable that the origin of any member was in the territory of the present neighbouring forms, although all may have been outside the present range of the group (i.e. when vegetation belts were pushed north or south).

In such a contingency each proto-species may be presumed to have held approximately the same position in regard to its neighbours as it does at present.

CHARACTERS

The study of the francolins in species groups has served to demonstrate that many characters which might be considered as guides to relationship show variable degrees of uniformity in each group. For example, in the Bare-throated Group the extent of bare skin on the face and throat is absolutely constant, and can be regarded as a "group character", whereas in other groups closely related species may have a variable amount of bare skin. It seems useful therefore to discuss some of these characters separately at the start in order to obtain an understanding of their importance. A summary of some of these characters is set out in Table 1.

SIZE

Little emphasis has been put on size or proportions in this paper, for though there is considerable individual variation there is reasonable uniformity in most related species. In the Red-winged Group the long-billed and short-billed populations of *F. shelleyi* provide the only example of marked proportional variation. On the whole general variation in size follows Bergmann's Law in relation to altitude and latitude, equatorial and lowland birds usually being smaller, but there are several inconsistencies. It is perhaps worth noting especially the incidence (for which I cannot account) of exceptionally small birds on the coasts of Kenya and southern Angola, and, to a lesser extent, Natal, since this feature is found in other genera besides francolins.

PLUMAGE

(a) *Feather patterns.* The complexity of the feather patterns has already been referred to. A number of examples are illustrated below which serve to define some of the descriptive terms I have used, and which have been arranged in sequences to indicate some of the transitional stages between one pattern and another. This is a subject which deserves fuller treatment than I can give it here and much of the discussion by Harrison in his paper "The incidence and origin of spotted patterns in the Estrildidae" (awaiting publication in the Ibis) is relevant to the francolins. It is sufficient here to emphasise that comparatively small changes in feather pattern,

SUMMARY OF SOME IMPORTANT CHARACTERS—TABLE 1

NOTES AND ABBREVIATIONS.

Column 1, *Size*. L—large, ♂ wing over 180 mm.; M—medium, 150–180 mm.; S—small, under 150 mm.

Column 2, *Sexual Dimorphism*. Species in which there is only a tendency for females to be more vermiculated are not shown as sexually dimorphic.

Column 3, *Bill*. u. m.—upper mandible; l. m.—lower mandible.

Column 5, *Normal Complement of Spurs*. Whole numbers indicate fully developed, sharp spurs; fractions indicate partly developed blunt spurs; "U" indicates an undeveloped spur evident as a swelling. When two spurs are present the lower is the longer unless otherwise stated. Numbers in brackets indicate that only a few sexed specimens have been examined.

Column 6, *Bare Skin*. Very small coloured patches behind the eye, or areas of dull bare skin are not shown.

Group	Species	1	2	3	4	5	6
		Size	Sexual Dimorphism	Bill	Legs	Normal Complement of Spurs	Bare Skin
SPOTTED	<i>francolinus</i>	M-L	yes	black/brown.	red/orange-brown	♂ $\frac{1}{2}$, ♀o	
	<i>pintadeanus</i>	M	yes	black/brown.	orange/yellow	♂1 small, ♀o	
	<i>pictus</i>	S-M	slight	black/brown.	orange/yellow	♂o	
BARE-THROATED	<i>leucoscepus</i>	L	no	black, red base.	black	♂1 $\frac{1}{2}$, ♀o	throat yellow, patch round eye, red.
	<i>rufopictus</i>	L	no	coral red.	brown	♂1 $\frac{1}{2}$, ♀o	throat and patch round eye, coral red.
	<i>swainsonii</i>	L	no	u. m. blackish. l. m. dull orange.	blackish	♂1, ♀o	throat and patch round eye, red.
	<i>afer</i>	M-L	no	red.	red	♂1-1 $\frac{1}{2}$, ♀o	throat and patch round eye, red.
	<i>erckelii</i>	L	no	black.	yellowish	♂2 (upper longest), ♀o	
MONTANE	<i>ochropectus</i>	L	no	u. m. black, l. m. yellowish.	yellowish	♂2 (upper longest), ♀o	
	<i>castaneicollis</i>	L	no	red.	red	♂2 equal, ♀o	
	<i>jacksoni</i>	L	no	red.	red	♂1 $\frac{1}{2}$, ♀o	eyelids, red.
	<i>nobilis</i>	L	no	red.	red	♂1 $\frac{1}{2}$, ♀o	patch round eye, red.
	<i>camerunensis</i>	M-L	yes	orange-red.	orange-red	♂1 $\frac{1}{2}$, ♀o	patch round eye, red.
	<i>swierstrai</i>	M-L	yes	orange-red.	red	♂1-1 $\frac{1}{2}$ (♀o)	
	<i>ahantensis</i>	M-L	no	orange, black base.	orange	♂1 $\frac{1}{2}$, ♀o	
	<i>squamatus</i>	M-L	no	orange-red, dark culmen.	orange-red	♂1 $\frac{1}{2}$, ♀o	
SCALY	<i>griseostratus</i>	M	no	u. m. blackish, red base, l. m. orange-red.	orange-red	(♂1), (♀o)	

Group	Species	I	2	3	4	5	6
VERMICULATED	<i>bicalcaratus</i>	M-L	no	greenish, black culmen.	greenish	♂1 $\frac{3}{4}$, ♀0	small patch round eye, yellow.
	<i>icterorhynchus</i>	M-L	no	orange, black culmen.	orange	♂1 $\frac{1}{2}$, ♀0	small patch round eye, red.
	<i>clappertoni</i>	M-L	no	black, red base.	reddish	♂1 $\frac{1}{2}$, ♀0	
	<i>hildebrandti</i>	M-L	yes	reddish, black culmen.	red	♂1 $\frac{1}{2}$, ♀1-1 $\frac{1}{2}$	
	<i>natalensis</i>	M-L	no (natalensis) slight (nearvi)	reddish brown.	dull red	♂1, ♀0	
	<i>hartlaubi</i>	S-M	yes	u.m. horn, l.m. yellowish.	yellow	♂2U, ♀1-2U	
	<i>adpersus</i>	M-L	no	orange-red.	orange-red	♂1, ♀0	eyering, yellow.
	<i>capensis</i>	L	no	u.m. brown, l.m. reddish.	orange-red	(♂1 $\frac{1}{2}$), (♀ $\frac{1}{2}$ -1)	
	<i>harwoodi</i>	L	?	red.	red	(♂1 $\frac{1}{2}$)	round eye, red.
	<i>sephaena</i>	S-M	slight	black.	dull red	♂1, ♀0	
STRIATED	<i>streptophorus</i>	M	no	u.m. black, l.m. yellowish.	dull yellow	♂1U	
	<i>psilolaemus</i>	M-L	no	blackish.	dull yellow	♂1, ♀0	
RED-WINGED	<i>shelleyi</i>	M	no	blackish, yellowish at base.	dull yellow	♂1, ♀0	
	<i>africanus</i>	M	no	blackish brown.	dull yellow	♂1 small, ♀0	
	<i>levaillantoides</i>	M	no	blackish brown, yellowish at base.	dull yellow	♂1 small, ♀0	
	<i>levaillantii</i>	M	no	blackish brown, yellowish at base.	dull yellow	♂ $\frac{1}{2}$ -1	
	<i>finchi</i>	M-L	no	blackish.	yellow	(♂ 1 small) (♀ $\frac{1}{2}$)	
	<i>coqui</i>	S-M	yes	black, yellow base.	yellow	♂1, ♀0	
RED-TAILED	<i>schiegeleri</i>	S-M	yes	black, yellow base.	yellow	♂1, ♀0	
	<i>albogularis</i>	S-M	yes	black, yellow base.	yellow	♂1, ♀0	
UNGROUPED	<i>lathamii</i>	S	yes	black.	yellow	♂1	patch, round eye, crimson.
	<i>nahani</i>	S	no	crimson, black tip.	crimson	♂♀ none	eyelids, green.
	<i>gularis</i>	M-L	no	black.	orange	♂1	
	<i>pondicerianus</i>	S-M	no	brown.	dull red	♂1	

particularly at the tip of the feathers, may greatly alter the appearance of a bird. (Compare the great differences in the general appearance of the breasts of a female *schlegelii* and a male *coqui*, and in the underparts of a male and female *pintadeanus* with the small differences in feathers 2 and 1, and 5 and 3 of Figure 1.)

(b) *Underparts*. The greatest variety of colour and pattern throughout the genus is found on the underparts (and to a lesser degree on the mantle) and considerable variation is found between closely related birds. The most striking example is illustrated by Bowen (1930) and shows the difference between the subspecies of

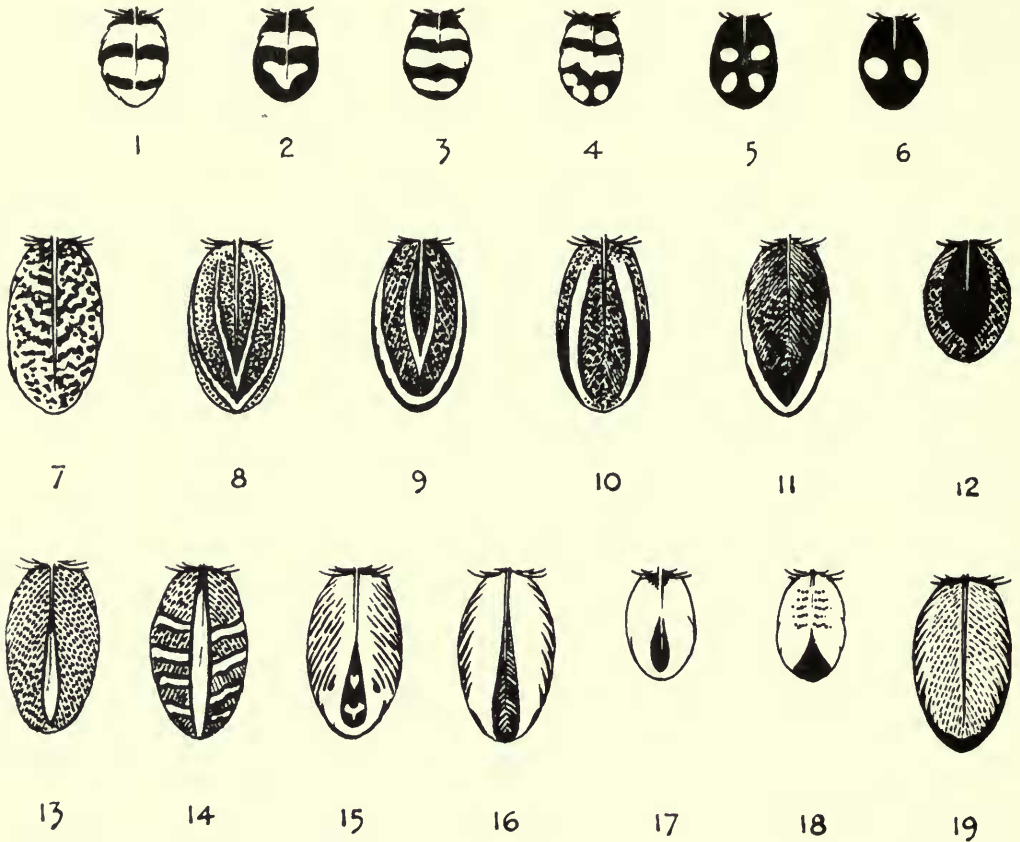


Fig. 1. Feather patterns.

1. Barred (*♂ coqui*, breast).
2. Barred with inverted triangle at tip (*♀ schlegelii*, breast).
3. Transition, barred to spotted (*♀ pintadeanus*, breast).
4. Transition, barred to spotted (*♂ shelleyi*, breast).
5. Transition, barred to spotted (*♂ pintadeanus*, breast).
6. Spotted (*♂ francolinus*).
7. Vermiculated (*hildebrandti*, back).
8. Irregular double-V-pattern (*harwoodi*, back).
9. Double-U-pattern (*clappertoni*, back).
10. U-pattern (*clappertoni*, back).
11. V-pattern (*clappertoni*, back).
12. Scalloped (*camerunensis*, back).
13. Striated (*sephaena*, back).
14. Quail-patterned (*shelleyi*, back).
15. Drop-shaped pattern with windows (*bicalcaratus*, breast).
16. Streaked (*jacksoni*, breast).
17. Drop-shaped pattern (*clappertoni*, breast).
18. Triangular pattern at tip (*sephaena*, breast).
19. Scaly (*squamatus*, breast).

F. afer with vermiculated underparts which hybridise freely with those with streaked underparts.

(c) *Upperparts*. The upperparts are basically either plain, streaked, vermiculated or "quail-patterned" (Fig. 1, 14), sometimes with a more complicated mantle patterning. While related species may vary between plain, streaked and vermiculated (see Montane Group) "quail-patterning" is more constant throughout the three groups in which it is found.

(d) *Wings and Tail*. The wings and tail are, on the whole, not conspicuously patterned or coloured, exceptions being found in the red wings of the Red-winged Group and some of the Red-tailed Group, and in the tails of the Red-tailed and Striated Groups which are reddish and black respectively.

A further exception is the light wing patch under the wing of *leucoscepus*, and rather similar light colour in the wings of *clappertoni*, which are the only members of their respective groups to have this character. These patches may have functional significance, for Harrison tells me he has observed the bare-throated *leucoscepus* in the London Zoo displaying with its wings carried forward exposing the light patch. Since other bare-throated francolins have plain wings it would be interesting to know if they have a different display, and also whether *clappertoni* and red-winged birds display in the same way.

(e) *Facial pattern*. Facial pattern seems to be an important character since it is the only feature of adult plumage which is recognisable in the chicks (see below), yet again related species show no constancy. In the Spotted Group two members have conspicuous facial patterns but *pictus* is unpatterned (yet hybridises with *francolinus*): in the Red-tailed Group the male *coqui* is unpatterned but the female patterned, the two sexes being recognisable in the chicks: in the Red-winged Group *finschi* is unpatterned but all other members have a black bridle and necklace, either well defined or indicated by spotting. Unfortunately chicks of many of the critical species are not available.

It has proved impossible to include a summary of plumage in Table 1, since the variation in colour and pattern is too complex to put into a few words. In the text I have tried to give sufficient descriptions to enable the reader to form a picture of the bird but without going into full detail.

SEXUAL DIMORPHISM

As a rule in francolins the sexes are alike except that the male is more heavily spurred and the female often slightly more vermiculated, but there is marked sexual dimorphism in all members of the Red-tailed Group: in two out of nine members of the Vermiculated Group, one of which hybridises, and in part intergrades, with another member in which the sexes are alike: in two out of three members of the Spotted Group: in two out of seven members of the Montane Group, and in *lathamii*.

EXTENT OF BARE SKIN

Bare skin on the throat as well as round the eye is found only in members of the Bare-throated Group (though not in the chicks). Various other species scattered

through different groups have conspicuous bare patches round the eye, namely *camerunensis* and *nobilis* in the Montane Group, *harwoodi* in the Vermiculated Group, and *nahani*. Others have smaller patches (*clappertoni*, *icterorhynchus*, and *adpersus* in the Vermiculated Group)—or coloured eyelids (the montane *jacksoni*)—or small coloured patches behind the eye. Unfortunately these smaller patches have largely been ignored by collectors especially when they are not brightly coloured and it is difficult to ascertain from skins in which species they are present, or if colouring is seasonal: to avoid error only conspicuous areas of coloured skin are therefore mentioned in the table.

COLOUR OF BILL AND LEGS

This is a character that is reasonably constant in half the groups but very variable in the others, striking variation being found between the three northern species in the Vermiculated Group which otherwise form a remarkably homogeneous assemblage.

SPURS

The number of spurs carried by males and females in any species is not constant, and indeed has been known to differ on the two legs, nevertheless there is sufficient constancy to justify the term "normal complement". This varies between species, from a complete lack of spurs in either sex in *pictus* of the Spotted Group and *nahani* to two fully developed spurs in the males of *erckelii* in the Montane Group. Blunt, half-developed spurs are found even in adult birds, often in males as an upper spur, and occasionally in females of almost all species that are normally without spurs. In the rare cases where a bird has a normal complement of two fully developed spurs it seems that the upper is likely to be equal to or longer than the lower, but in the cases where a bird has one fully developed and one half-developed spur it is the lower which is fully developed and therefore the longer. Undeveloped spurs are indicated by swellings and are found normally in fully adult males of the vermiculated *hartlaubi*, and the striated *streptophorus*. It can be said, therefore, that the number of spurs has some taxonomic significance, but is not as infallible or as important a character as some text books lead students to believe.

FIELD HABITS

I have too little personal experience of francolins in the field and too little has been written, especially of some of the rarer species, for me to make much use of habits and behaviour as criteria of relationship. There is a certain amount of information on whether or not the birds are found in coveys, and whether they perch or roost in trees, but no one group is fully documented. It can be said confidently, however, that the majority of francolins are found in pairs or small coveys according to the season, but four species at least are more gregarious: in the Vermiculated Group *bicalcaratus* is found in coveys of up to 40 birds (Bannerman, 1930: 321), and *adpersus* up to 20 (McLachlan & Liversedge, 1957: 96): and in the Red-winged Group *africanus* is found in coveys up to 30 birds (Horsburgh, 1912: 47), and

levaillantoides up to 14 (op.cit.: 54). I have found definite records of most members of the first five groups taking to trees though they do not necessarily use them regularly for roosting: Hopkinson (1923: 128) found *bicalcaratus* roosted in trees only in the rains, and this may well be true of other species. On the other hand I have no records of any members of the last three groups, the Striated, Red-winged and Red-tailed, taking to trees even when alarmed and it would seem that these birds, with their more cryptic ("quail-patterned") coloration rely for protection on sitting close.

HABITAT

It will be shown in the discussion on the groups that the majority of the francolins have very precise ecological requirements, so much so that, though several different species may be found in the same area, it is rare to find two different species on the same ground. For instance at Onguati in South West Africa *F. adspersus*, *F. levaillantoides* and *F. hartlaubi* were found within a few hundred yards of each other, but *adspersus* was strictly confined to the riverine vegetation, *hartlaubi* to the rocky kopjes and *levaillantoides* to the grasslands between (Macdonald, 1957: 52). Similar instances are found throughout southern and eastern Africa where the ranges of six groups overlap but there are also exceptions. Pitman has found *coqui*, *levaillantii* and *afer* on the same ground in Uganda: Elliot also has found *coqui* with other species in Tanganyika and Blasdale has found it with *bicalcaratus* in Nigeria (but not with *clappertoni*): Benson and Stuart-Irwin have found *natalensis* and *sephaena* together in riverine thickets in both Northern and Southern Rhodesia, and Stuart-Irwin tells me that *sephaena* is also found with *adspersus* in Ngamiland, though in Southern Rhodesia the two would never occur together: *adspersus* also occurs with *swainsonii*, sometimes in the same flocks, in Ngamiland. All these examples are of members of different groups occurring together but hybrid specimens show that members of the same group may mix where they have a common boundary, as indeed would be expected.

In any one group the different species may all share the same, or very similar, ecological preferences, as in the Spotted and Scaly Groups, or different species may have different preferences, as for example in the Red-tailed and Bare-throated Groups. There are also individual species which show a wide choice of habitat in different parts of the range, most notably the red-winged *F. shelleyi* and the red-tailed *F. coqui*, and similar inconsistency is shown in the altitude at which some species are found, especially among all members of the Red-winged Group (except the Montane Redwing, *F. psilolaemus*) and in *F. squamatus* of the Scaly Group.

VOICE

It would seem that voice should be a guide to relationship in the francolins but the few direct comparisons that have been made between species indicate that there are unexpected inconsistencies and affinities. Benson, for instance, records a remarkable difference in the call of *sephaena* in Abyssinia and Rhodesia (1958: 191), yet considerable uniformity in both *levaillantii* and *coqui* between the calls of north

and central African birds (1948: 52). He tells me also that there is a marked family resemblance in the voice of three members of the Red-winged Group, *levaillantii*, *shelleyi* and the Abyssinian *levaillantoides*, and in three members of the Bare-throated Group, *afer*, *swainsonii* and *leucoscepus*. Similarities between members of the Montane and Scaly Groups respectively have been recorded by Hall (1960a: 408) and Collier (1935: 666). Furthermore Chapin (1932: 715) found the call of the bare-throated *afer* indistinguishable from that of *icterorhynchus* of the Vermiculated Group. On the other hand Blasdale tells me that the red-tailed *coqui* and *albugularis* in Nigeria have quite different calls.

CHICKS

I have only been able to examine chicks of less than half the species and it is only possible therefore to draw a few general conclusions. The most striking variation is shown in the pattern of the crown and face, but in this respect there is little difference between the representatives examined of the Bare-throated, Montane, Scaly or Vermiculated Groups, all of which have a solid brown crown (sometimes edged black) and a single conspicuous brown or blackish stripe from the bill through the eye to the neck. In addition the only chick examined of the Montane Group (*erckelii*) has a short black stripe below the eye. The chicks of the Red-winged Group are distinctive in having a narrow and darker crown patch, bordered on each side by eight alternate white and black stripes over, through and under the eye, the forerunner of the adult bridle and necklace. Unfortunately no chick has been examined of *F. finschi*, the only member of the group without any black-and-white bridle or necklace, and none of *F. psilolaemus* in which the bridle is spotted and indistinct. The female *coqui* of the Red-tailed Group has a similar pattern to the red-winged chicks though less clearly defined, but the male chick is like those of the other groups, though with the brown of the crown extending further forward to the beak: the chicks therefore bring out the sexual dimorphism of the adults. The adults of the Spotted Group have, like those of the Red-winged Group, a very striking facial pattern, and the chicks have a similar narrow crown patch with alternate stripes on either side, but the pattern is paler than in the Red-wings and ill-defined. The chick of the ungrouped *pondicerianus* has an indefinite pattern intermediate between both main varieties, the dark stripes above the eye being incomplete and ill-defined. In view of the small variation evident between the chicks of many species and even groups, it is interesting to note that subspecific variation is apparent between the paler and darker races of *F. francolinus*, and between two "potential species" of the Red-winged Group *F. s. shelleyi* and *F. s. whytei*.

EGGS

The British Museum has a reasonably representative collection of francolin eggs, including those of at least one member of every group, but as a guide to relationship they are disappointing. All are rather broad, and are plain or lightly freckled, ranging in colour from white to light brown. Large series of eggs of both *F.*

bicalcaratus and *F. francolinus* show there is considerable variation in colour within a species, largely correlated with the darker and paler subspecies living in wetter or drier conditions. There is also some variation in shape. The eggs of the two African forest francolins *lathamii* and *nahani* are the most distinctive, those of *lathamii* (represented by two clutches from the Cameroons) being a plain reddish brown and more elongated than any others, and those of *nahani* (represented by one clutch from Uganda) being the most heavily freckled, brown on a buff ground. Pitman tells me that the eggs of *sephaena* are also distinctive in having an exceptionally hard shell.

THE SPOTTED GROUP (MAP 1) (*F. francolinus*, *F. pictus*, *F. pintadeanus*)

RANGE AND CHARACTERS

The Spotted Group is the only Asiatic group and is formed by three of the five Asiatic species. It ranges from south China and the Indo-Chinese countries through Thailand, Burma, the Indian sub-continent, Ceylon, Persia, Iraq to the eastern Mediterranean and Cyprus. There is evidence that it has also inhabited many of the Mediterranean countries and islands in historical times (Lilford, 1862, Lavauden, 1936). Its members are birds of grassland and scrub jungle, and are found also in cultivations where there is sufficient cover. They occur up to 5,000 ft. but commonly prefer lower altitudes.

They are mostly medium-sized, with the mantle either spotted or V-patterned in brown and buff and the back and tail narrowly barred in black and white, or buff and brown: the wings are barred or spotted. Below they are basically black or dark brown with white spots, but in the females of two of the species (*F. francolinus* and *F. pintadeanus*) these spots are merged together and elongated to form irregular bars. The under tailcoverts are maroon. The bills are black or dark brown and the legs vary from yellow to red-brown. Spurs are poorly developed, the normal complement for the males of *F. francolinus* and *F. pintadeanus* being one only, and that rather short and blunt, while *F. pictus* is without spurs in either sex.

SPECIES AND POTENTIAL SPECIES

The three recognised species are the only mainland forms with which we need be concerned for other variation is clinal and ecological and does not suggest that any smaller populations have been isolated for any length of time from the main body. The species are quite distinct: the western *F. francolinus* has marked sexual dimorphism, the male having the throat, breast and sides of face largely black, with sparse white spots on the side of the breast, and white cheeks: it has a complete broad maroon collar and some black feathers with white spots on the upper mantle; the rest of the mantle and wing coverts are V-patterned in buff, brown and occasionally black.

The female has no black, the throat being whitish, the sides of the face mottled brown and buff, and the underparts irregularly barred in brown and off-white.

The upperparts are patterned like those of the male but without black and with the maroon collar replaced by a small rufous patch on the hind neck.

The range of *F. francolinus* extends eastwards to Manipur. It is replaced in southern India by *F. pictus*, a smaller bird with little sexual dimorphism, but in females there is a tendency for the patterning on the abdomen to merge into bars and this seems most pronounced and most constant in the Ceylon population (*watsoni*). The face and throat of *F. pictus* are unpatterned and rich ochre in colour: the upperparts are similar to those of the female *F. francolinus* but with more spotting in the mantle and no rufous collar patch: the underparts are intermediate between the male and female of *francolinus* being basically black, or very dark brown, regularly covered all over with large buff spots.

Where the ranges of the *F. francolinus* and *F. pictus* meet in Rajasthan (Rajputana), Uttar Pradesh (United Provinces) and Bihar there is no natural barrier between them, and no ecological distinctions have been noted. It is evident that they do not interbreed freely but do so occasionally for there are four specimens in the British Museum which appear to be hybrids: these are from Deesa (the type of *F. intermedius*), "Neemsar" (an unplaced locality probably, from the history of the collector, near Fateghur) and "Bihar" (no detailed locality).

Ceylon birds are not very different from those of the mainland, but are rather darker and more closely patterned, with the tendency (already noted) for the females to be slightly barred on the abdomens.

East of Manipur *F. francolinus* is replaced by *F. pintadeanus* which, in both sexes, differs from the other two species in having the throat and cheeks white, sharply divided by a black line, and having the mantle largely spotted, not V-patterned, and with a considerable amount of rufous, especially in the male. Below the male is patterned all over like *F. pictus*, but with the spots pure white on a deep black ground; the female is barred like the female of *F. francolinus* but with the barring narrower and more sharply contrasted.

The higher ranges of Manipur and the Chin Hills seem to form an effective barrier along most of the boundary between *F. pintadeanus* and *F. francolinus* though they might be expected to meet along the coastal strip. I know of no records of hybridisation between them.

OTHER VARIATION

Variation is clinal. In *F. francolinus* western birds are large and dark (*francolinus*), grading through *arabistanicus* of Persia and Iraq to the small, pale, grey birds of Baluchistan and western India (*henrici*). Birds of north-eastern India are darker again (*asiae*) grading into the very dark *melanotus* of Assam.

In *F. pictus* there is a pale population in the drier north-western areas (*pallidus*) and other mainland birds (*pictus*) are intermediate between *pallidus* and the darker Ceylon birds (*watsoni*).

In *F. pintadeanus* birds from southern China and northern Indo-China are paler, less heavily patterned than those of Burma and Thailand (*phayrei*).

EVOLUTION

The Spotted Group presents a straightforward pattern of three allopatric species with a continuous distribution across sub-tropical Asia. To interpret this pattern

it is only necessary to visualise less favourable conditions in the northern parts of the present range which would serve to isolate the three species from each other.

I suggest therefore that the three species have arisen from a single species occupying the present range of the whole group, and possibly much of southern Europe as well. In an unfavourable era, such as a Glaciation, conditions in the northern parts of the range became unsuitable and *proto-francolinus* was isolated in Palestine and possibly Arabia (if the era was wet as well as cold): *proto-pictus* was isolated in southern India and *proto-pintadeanus* was isolated in south-eastern Asia (Map 1A). With the return of favourable conditions the three species spread north again, *proto-francolinus* invading India from the west and establishing itself north of *proto-pictus*. In the period of isolation speciation had developed sufficiently for the three species not to interbreed freely when they rejoined, but the presence of hybrids on the boundary between *francolinus* and *pictus* indicates that genetic isolation is not absolute.

A summary of the evolution postulated is, therefore, as follows:—

Stage 1. The ancestral form of the group widespread, covering present range and possibly southern Europe as well.

Stage 2. An unfavourable era, probably a Glaciation, pushes the range southwards isolating the ancestral stock of the three species in south-western Asia, southern India, and south-eastern Asia (Map 1A).

Stage 3. With the return of more favourable conditions the group spreads northwards again, but speciation had advanced sufficiently in the three isolated blocks to inhibit free interbreeding when they rejoin.

THE BARE-THROATED GROUP (MAP 2)

(*F. afer*, *F. swainsonii*, *F. rufopictus*, *F. leucoscepus*)

RANGE AND CHARACTERS

The Bare-throated Francolins are widespread in eastern Africa from Eritrea to Cape Province and westwards, south of the Congo forest, to Gabon, Angola and northern South West Africa. They are found at comparatively low altitudes, usually near water-courses or in grasslands with cover of trees and scrub in which to hide.

They are large francolins distinguished by having a conspicuous patch of bare skin on the throat and round the eye, varying in colour from scarlet to yellow. The bill and legs vary from red to black (never yellow): spurs are fairly well developed, the males of all species having normally a long and strong lower spur; a short blunt upper spur is found commonly in two of the species (*F. leucoscepus* and *rufopictus*), less often in *F. afer* and rarely in *F. swainsonii*. In the group as a whole the upper parts are plain brown from the crown to the tail, with some darker centres to the feathers of the mantle and a few light vermiculations, but in one species (*leucoscepus*), the mantle feathers have white shaft streaks, and in another (*rufopictus*) they have broad rufous edges. The underparts are, on the whole, streaked, but vary widely in colour and in the amount of vermiculation. The sexes are alike except that the females tend to be slightly more vermiculated.

SPECIES AND POTENTIAL SPECIES

The Bare-throated Group is a far more complicated assemblage of forms than the distribution of the four species suggests, for variation in colour and pattern among the populations of *F. afer* shows it has had a turbulent history and that at some time at least six of its subspecies have been isolated for a sufficient period for them to have diverged considerably.

The species themselves are largely allopatric and ecologically segregated, overlapping only in a few marginal areas. The most distinctive member of the group (*F. leucoscepus*) is confined to the acacia steppe of the north-east (Map 11, Type 25). In *leucoscepus* the bare skin is red round the eye, yellow on the throat, the bill black with a red base and the legs black: the mantle has white shaft-streaks and the underparts are irregularly streaked all over with plain brown and white, each feather being brown with narrow white edges and a triangular white patch at the tip, tapering up the shaft: there is a faint rufous tinge in the brown parts of many feathers. The primaries have some white on the inner wings which forms a conspicuous patch when the wing is displayed: there is no comparable patch in other members of the group.

F. leucoscepus is replaced by another species, *F. rufopictus*, in a small area of Tanganyika stretching from the south-eastern shore of Lake Victoria to the Wembere.¹ This area is still within the dry belt of acacia steppe but differs from typical *leucoscepus* country in the types of *Acacia* species present (Stronach *in litt.*), so it may possibly form an ecological island particularly suited to *rufopictus*.

In *rufopictus* the bare skin is coral red, the bill is red and the legs brown: the feathers of the upperparts are basically grey-brown with dark vermiculations and dark shaft-streaks, with the feathers of the mantle and wing coverts broadly edged with chestnut: the breast is mainly grey with black shaft-streaks and the rest of the upperparts streaked black, white and chestnut; the eye-stripe and sides of the face are black and white.

In southern Africa there is a third species (*F. swainsonii*) associated chiefly with acacia country, ranging in the acacia/mopane savanna belt (Map 11, Types 20 and 22) from South West Africa to Mozambique and extending up the Loangwa valley to the Nyasaland border. In Southern Rhodesia, however, it is found scattered through the grasslands of the woodland belt, eastwards to the Mashonaland plateau.

In *F. swainsonii* the bare skin is red, the bill black above and orange below, the legs black, with the single spur in the males very long and strong: both above and below it is a pale brown with some darker shaft-streaks; it has a faint grey wash over the breast and chestnut streaking on the abdomen. Populations of the Transvaal and southern Southern Rhodesia (*F. s. swainsonii*) have a blackish mottled patch on the abdomen.

The fourth species, *F. afer*, inhabits rather wetter areas than the other three. Throughout central Africa its range coincides with the extent of the woodlands,

¹ I can find no confirmation, either from museums or from field workers, of the statement by Van Someren (1925: 99) that *F. rufopictus* occurs in Ruanda. No actual specimens or localities were quoted.

except in western Southern Rhodesia where these are occupied by *F. swainsonii* (see above), and in southern Angola where it has intruded into a small area of the acacia belt. In South Africa there are two isolated populations in the south-eastern Transvaal and in the coastal strip of southern Natal and Cape Province.

In *F. afer* the areas of bare skin, the bill and the legs are red: the back is plain brown with some darker feather centres. The sides of the face and the underparts show considerable variation and two diverse blocks of subspecies are easily recognised, separated by two areas of hybridisation. The first block comprises all the populations of the southern Congo, northern Angola, Northern Rhodesia east to the Muchinga Escarpment, extreme western Tanganyika, Uganda and the shores of Lake Victoria. These birds are heavily vermiculated on the underparts, with sparse chestnut streaks on the abdomen: the feathers of the face are minutely patterned in black and grey. I can recognise no significant geographical variation throughout this area and all populations may be referred to *F. a. cranchii*, except for some very dark birds in the Ruzizi valley, north of Lake Tanganyika (*harterti*) in which the streaks on the abdomen are maroon rather than chestnut; also the populations bordering on the hybrid zones in Northern Rhodesia and Tanganyika have a mixture of white in the abdomen (*F. a. intercedens*).

In the second block the birds have no vermiculation and are strongly patterned in black, white and grey on the face and underparts, and only the subspecies of south-eastern Cape Province has any chestnut or maroon. The black-and-white subspecies have a broken distribution, one, *F. a. afer*, being restricted to the south-western corner of Angola along the Escarpment and in the Cunene basin. In *F. a. afer* the face is white and the underparts broadly streaked in white and black, the feathers having black centres and white edges.

The rest of the block is found in the eastern half of the country and comprises an assemblage of subspecies north of the Limpopo and two isolated populations in South Africa. The northern birds all have the feathers of the breast grey with black shaft streaks contrasting with the feathers of the abdomen, which are mainly plain black, and those of the flanks which are streaked black and white. Birds of the coastal population of Kenya (*leucoparaeus*) have the eyestripe black and white and the sides of the face white. They are replaced in northern Tanganyika by birds with a wholly black face, and similar birds are found south to southern Nyasaland and extreme south-eastern Northern Rhodesia (*melanogaster* and *loangwae*). There is no information as to whether or not there is intergradation between *leucoparaeus* and *melanogaster* but birds typical of these forms are found within 110 miles of each other at Mombasa and Korogwe respectively.

Birds from the eastern districts of Southern Rhodesia and southern Portuguese East Africa have the whole face and a necklace above the breast white (*swynnertoni*). In the lower Zambezi valley, the Salisbury area of Southern Rhodesia, and in southern Nyasaland, between the ranges of the black-faced and white-faced forms, there is an unstable population with a variable amount of black and white in the face (*humboldtii*).

Birds of the isolated population in Natal and Cape Province are again differently patterned, having the face wholly black, and the underparts from the upper breast

to the abdomen streaked with white, maroon and black, the white lying in parallel streaks on either side of the shaft (*castaneiventer*). These birds intergrade in the region of Uitenhage with the populations of the southern Cape in which the maroon is wholly replaced with black (*notatus*).

In Natal Vincent tells me that *castaneiventer* is found only between 2,000 and 4,000 ft., usually on the edges of evergreen forest. It is absent from northern Natal and the coastal belt (where its place is possibly taken by *F. natalensis* of the Vermiculated Group). There is, however, an isolated population in the south-western Transvaal (*lehmanni*) which is intermediate in some respects between the *castaneiventer/notatus* forms and *swynnertoni*, having the face black and the abdomen with long parallel white streaks as in *notatus*, but the whole breast grey, with black shaft streaks, contrasting with the abdomen as in *swynnertoni*.

Between the block of vermiculated and chestnut forms in the north and the blocks of black-and-white forms in the east and in southern Angola there are two hybrid zones, one stretching from Kondoa and Dodoma in central Tanganyika through central Nyasaland into the Luangwa valley, the other through northern and central Angola into extreme north-western Rhodesia. The hybrid populations of Tanganyika and Nyasaland have well-defined streaks on the abdomen varying in the proportion of chestnut to black-and-white according to the proximity of the respective parent forms, but most birds from the same area are reasonably constant and can be distinguished from birds of other local populations. This does not seem to be true in Angola where micro-populations show greater variability, and the streaking on the abdomen is less regular and less defined.

In Kenya and Tanganyika *F. afer* replaces *F. rufopictus* and *F. leucoscepus* without apparently any overlap, but its relations with *F. swainsonii* in southern Africa vary. In the Luangwa valley, where both occur, *F. afer* is found chiefly in the riverine vegetation and *F. swainsonii* in the acacia and mopane (Benson and White, 1957: 23) and the same applies in the Namwala, Mumbwa and Lusaka districts (Benson). The same is probably true in the Zambezi and Limpopo valleys. However, in Southern Rhodesia where *F. swainsonii* has intruded into the woodland belt the two come together without any ecological segregation, so that both occur on the same ground.¹ In this area two birds have been collected which show characters of both species, one from near Salisbury (the type of *Pternistis cooperi*, Roberts, 1947) and the second from Hartley's Farm, Rusape, where both species are found (Smithers, *in litt.*). Other specimens of *F. afer* from the same farm have been noted to have dark brown instead of the normal red legs. This suggests strongly that some hybridisation takes place along this border.

There is a record of a third specimen which shows characters of both species (Markus, 1959), but this was collected at Francistown, three hundred miles from the nearest race of *F. afer*, or from any suitable habitat. It was unfortunately not preserved, but Markus (*in litt.*) described it as having a red bill and legs, no white on the face, but both white and chestnut markings on the abdomen, the white markings being like those of *F. a. lehmanni* and the chestnut like those of *F. swainsonii*.

¹ Smithers tells me that, with the clearing of land for farming, *F. swainsonii* has entirely replaced *F. afer* in parts of the Salisbury area within the last fifty years.

Since it is unlikely that there is an isolated population of *F. afer* in country that is both unsuitable and reasonably well known ornithologically, it must be regarded as an aberrant specimen of *F. swainsonii*, emphasising the close relationship of *afer* and *swainsonii*.

The exact ranges of *F. afer* and *F. swainsonii* in southern Angola are not known, nor is there any information on their relationship.

OTHER VARIATION

In *F. leucoscepus* variation is slight. Birds of the coastal areas of Eritrea and western Somaliland (*F. l. leucoscepus*) have rather more white on the feathers of the underparts than birds from other parts of the range (*F. l. infuscatus*), but elsewhere variation in the general darkness or paleness and degree of patterning of populations is sporadic in local populations.

Apart from the dark birds of the Transvaal and southern Southern Rhodesia (*F. s. swainsonii*) which have a mottled black patch on the abdomen, the variation in this species is linked with ecology. Eastern birds (*lundazi* White, 1947) are rather browner, less grey than those of the semi-desert areas of northern Bechuanaland and northern South West Africa (*gilli*) while another rather browner population may be recognisable from the Waterburg area (*damarensis*). (Hall, 1956: 100, Benson & White, 1957: 23, 138). Southern birds average larger.

In the stable populations of *F. afer* there is little variation that has not yet been discussed, but in the black-bellied, black-faced populations there is some clinal variation, birds of Tanganyika (*melanogaster*) being paler and less brown than those of Nyasaland and Northern Rhodesia (*loangwae* Grant & Praed, 1934).

EVOLUTION

The pattern presented by the Bare-throated Group is complex, for not only is there evidence of considerable hybridisation taking place at present but the morphological characters of the different species, and the degree and type of variation among the subspecies, suggest incidences of past hybridisation as well. A simple sequence of evolutionary stages is therefore difficult to envisage and it is perhaps best to start by discussing the features of the pattern that can be readily interpreted. It is apparent, for instance, that the present is a favourable era for *F. afer* since the hybrid zones indicate that it now occupies areas from which it has recently been absent. The diverse characters of the *afer* subspecies point to a lengthy period in which the two blocks of vermiculated and black-and-white subspecies were isolated from each other. Since neither apparently developed ecological preferences in that period they were able to interbreed when the ranges rejoined. Similarly the variation between many of the black-and-white populations points to periods in which they have been isolated.

Comparison between Map 2 and the vegetation map shows that the ends of the hybrid corridor through the Luangwa valley and central Tanganyika coincide with the intrusive tongues of acacia into the woodland belt. This suggests that the two *afer* blocks were divided from each other in a dry era when this corridor was wholly covered by acacia and occupied by the acacia species. It seems probable that dry conditions prevailed at the same time in most of Angola eliminating *afer* from the present hybrid zone and isolating the small population in the south in the region of the Angola escarpment where moister conditions might still be expected through proximity to the sea (see Hall, 1960). Similar dry conditions would serve also to split the eastern populations.

It is more difficult to visualise the conditions in which the four species were originally isolated from each other, and particularly so in the case of *afer* and *swainsonii*, which now occupy neighbouring vegetational zones with a common boundary of 10,000 miles. These two species seem to be the most closely related since they are alike above and in the colour of the bare skin; furthermore they apparently hybridise now in one limited area and the dark patch on the abdomen of *F. s. swainsonii* may be an indication of more extensive hybridisation in the past. They may therefore be assumed to have separated most recently. Conversely the distinctive *F. leucoscepus* was probably the first to be split from the ancestral stock of the group. *F. rufopictus* in some ways combines the characters of the other three species, having vermiculated, chestnut, white and black patterning in the feathers and having the bare skin orange, rather than yellow or red. It is possible that it may represent a relict population approximating more closely to the ancestral form of the whole group, or else be a product of past hybridisation between species that has become stabilised and established itself in an ecological island. Both these alternatives are very speculative and in selecting the latter as slightly more probable I have been guided by the resemblance of *rufopictus* on the underparts to some of the hybrids between the main blocks of *afer* subspecies. Its present distinctiveness and ability to live alongside both *leucoscepus* and *afer* without interbreeding suggest an early origin, probably before *afer* and *swainsonii* diverged.

I would postulate therefore that the bare-throated francolins were originally birds of acacia and that they were first split by a spread of woodland or forest into a north-eastern population (proto-*leucoscepus*) and a southern population (proto-*afer/swainsonii*). Later the two rejoined briefly and hybridised forming proto-*rufopictus*, a relict population which was left in Tanganyika in a subsequent wetter era when *leucoscepus* withdrew further north and proto-*afer/swainsonii* further south.

It is necessary now only to envisage some circumstances in which *afer* and *swainsonii* could develop. I can suggest no likely vegetational changes that would form a west-east barrier on similar lines to the present boundary, and conclude that they were split originally into an eastern population (proto-*afer*) and western population (proto-*swainsonii*) divided by a barrier of forest through Natal and the eastern districts of the Transvaal and Southern Rhodesia. In isolation proto-*afer* became adapted to wetter conditions and independent of acacia so that in a subsequent period was able to spread across to Angola through the woodland belt. It may have hybridised with *swainsonii* to a limited extent in the east but, for the most part, was ecologically segregated. It may also have hybridised to a limited extent with *rufopictus*, giving northern birds a higher proportion of chestnut and vermiculations in the feathers than the southern. (This is a possible way to account for the different directions in which the northern and southern blocks of *afer* diverged.) No subsequent changes affected the status of the four species and only *F. afer* was subject to further splitting and rejoining, though the ranges of the others would have spread and contracted in alternate dry and wet spells. It has already been suggested that a dry spell with a spread of acacia was responsible for isolating the two main blocks of *afer* subspecies and also the small population in southern

Angola. This diverged from the northern block along much the same lines as the southern block in the east, with black-and-white pattern predominating. Subsequently minor fluctuations would serve to isolate the various eastern populations of *afer* producing the subspecies *leucopareus*, *melanogaster*, *swynnertoni*, *castaneiventer* and *notatus*. In South Africa the population of the Transvaal (*lehmanni*), intermediate between *swynnertoni* and *castaneiventer*, may have once formed part of cline between them but has been isolated from both, possibly by the intrusion of *F. natalensis* of the Vermiculated Group.

A summary of the evolution postulated is therefore as follows:—

Stage 1. The group widespread in acacia.

Stage 2. The group split by a spread of forest, proto-*leucoscepus* isolated in the dry north-east, proto-*afer/swainsonii* in the south.

Stage 3. Less humid: the two populations rejoin briefly and hybridise producing proto-*rufopictus*. Proto-*afer/swainsonii* spreads across the southern part of the continent.

Stage 4. Proto-*swainsonii* in the west is separated from proto-*afer* in the east by a barrier of forest. In isolation proto-*afer* becomes adapted to wetter conditions (Map 2A).

Stage 5. Proto-*afer* spreads across to Angola through the woodland belt, possibly hybridising to a limited extent with both *swainsonii* in the south-east and *rufopictus* in the north.

Stage 6. In dry conditions *afer* is divided into two main blocks, one in the north and one in the south-east, with a small population isolated in southern Angola. In isolation the northern block develops distinctive chestnut and vermiculated patterning below, and the two southern populations a black-and-white patterning (Map 2B).

Stage 7. Minor fluctuations isolate the various eastern populations of *afer*.

Stage 8. A favourable era for the group as a whole and particularly for *afer*, the vermiculated and the black-and-white blocks of subspecies rejoining and interbreeding forming hybrid zones in the east and west. Among the eastern black-and-white subspecies the white-browed *swynnertoni* and the black-browed *melanogaster* meet and hybridise in the lower Zambezi valley.

THE MONTANE GROUP (MAP 3)

(*F. erckelii*, *F. ochropectus*, *F. castaneicollis*, *F. jacksoni*, *F. nobilis*, *F. camerunensis*,
F. swierstrai)

RANGE AND CHARACTERS

The Montane Group, as its name implies, is formed of scattered communities in the mountains of north-eastern Africa from Eritrea to Mount Kenya, on the eastern Congo border, in the highlands of Angola, and on Cameroon Mountain. Its members are birds which require some trees for cover and roosting and the majority of species are found in or near montane evergreen forest: only members of the northern species (*F. erckelii*) are less associated with forest being found on the grasslands of the high plateaux of northern Abyssinia where there are neighbouring woods.

In appearance this is the least homogeneous of the groups, so much so that it is

impossible to designate any "group" character other than that the males have the crown, lower back, primaries and tail plain brown or red-brown, and the females, in the species in which they are unlike the males, have the primaries, lower back and tail vermiculated. However, variation in the other characters seems to follow geographical trends, the birds of the extreme north-east being the largest and most heavily spurred with dark bills, yellowish legs, no bare skin round the eye and with the sexes alike, or only very slightly differentiated by a tendency for the females to have some vermiculations on the wing and tail. Birds of the two isolated western populations are the smallest, least heavily spurred with red bills and legs, and with the sexes quite unlike: in the Cameroon population there is an extensive area of red bare skin round the eye. The central species have some characters in common with one or both of their nearest neighbours so that all are linked. The variation in the colour and pattern of the underparts is considerable, but no more extreme than that found in one species (*F. afer*) of the Bare-throated Group. Taking these factors into account, together with the affinities of other birds and plants of the same montane communities, I am confident that it is correct to regard the montane francolins as a superspecies.

SPECIES AND POTENTIAL SPECIES

F. erckelii is the northern representative of the group and has a fairly continuous distribution in the grasslands of the Abyssinian massif from the Addis Ababa area northwards to southern Eritrea. An isolated population (*pentoni*) is found in the Red Sea Hills at Erkowit, which differs only in being rather greyer. *F. erckelii* is rarely found below 6,000 ft. and ranges up to 10,000 ft. It appears to be less dependent on the presence of evergreen forest than other members of the group, which would account for its more continuous distribution, and this continuity is reflected in the birds themselves, which are remarkably uniform in colour and pattern.

It is the largest of the francolins, with a black forehead and eyestripe, chestnut crown, the mantle and breast largely grey with maroon streaks and the rest of the underparts white with maroon streaks: the sexes are alike: the bill is black and the legs yellowish, the male having two spurs of which the upper is the longer.

On the Plateau du Day in (French) Somaliland there is an isolated population (*F. ochropectus*) living in the juniper forest above 3,500 ft. (Dorst & Jouanin, 1950). It is similar to *F. erckelii* in many respects of pattern but is dull in colour having the maroon and chestnut replaced by ochre or brown, and it has some U-patterning on the lower mantle: the bill is blackish with some yellow on the lower mandible: the legs are similar in colour and spurs to *F. erckelii*. It is in fact intermediate in many respects between *erckelii* and *F. castaneicollis* of southern Abyssinia but possibly sufficiently distinct from both to be granted specific rank.

The nearest population of *F. castaneicollis* is found within 150 miles of *F. ochropectus* in the mountains of western (British) Somaliland. Other populations are found in the massif of the Arussi plateau in Abyssinia east of the Rift, and in the montane "islands" over 6,000 ft. in southern and south-western Abyssinia.

It is apparently more dependent than *F. erckelii* on cover such as juniper and other evergreen forest and bamboo and, since forested patches over 6,000 ft. may be widely separated by unsuitable country, the range is very broken. In conditions such as these divergence between populations is to be expected and the species is, in fact, very variable, though individuals from the same populations are reasonably uniform allowing for the complex patterning of the feathers.

The species as a whole differs from *erckelii* and *ochropectus* in having a red bill and legs, the upper spur equal to or shorter than the lower. It has less black on the face and forehead, some U-patterning on the feathers of the mantle and breast and the abdomen largely white. In all the birds of the Arussi plateau south to Algehe (*F. c. castaneicollis*) this U-patterning is extensive on the back, wing-coverts and breast and clearly defined in black and white, mixed with some ochre and chestnut: Somali birds are similar but rather greyer (*ogoensis*). Birds from all the isolated populations west of Lake Zwai vary slightly (but may be grouped for convenience as *F. c. kaffanus*) but the U-patterning in all is less well defined and less extensive and the ochre is largely replaced by rich chestnut. An isolated population at Mega (*atrifrons*), less than 50 miles from Algehe where *F. c. castaneicollis* occurs, is quite unlike, being without any strong colour or pattern, the U-patterning being only faintly defined in brown and buff, and the throat and abdomen cream instead of white. This, like *ochropectus*, is a population whose taxonomic rank is questionable but Benson (1945: 393) found it was similar in habits, environment and voice to other forms of *F. castaneicollis* and it is therefore perhaps best regarded as a subspecies in spite of its very distinctive appearance.

There are unaccountably no representatives of the group in the juniper forests at Yavello (Benson, *op. cit.*), or apparently on the mountains of the southern Sudan, Uganda and northern Kenya (though they may possibly have been overlooked on the lesser known mountains, and unidentified francolins have been recorded from Mt. Kulal and Mt. Nyeri at the southern end of Lake Rudolf) but in the Aberdare Highlands and on Mount Kenya *F. jacksoni* is common near the edge of the forest and in the bamboo above 7,500 ft. It has also been found twice west of the Rift on the Mau Escarpment and in the Cherangani Mountains. It is very similar to the more chestnut and less heavily patterned populations of *F. castaneicollis* found in the west, but has the wings, back and tail a brighter more rufous brown, and the feathers of the upper mantle, breast and abdomen chestnut edged with white, with no black and white U-patterning. *F. jacksoni* has a scarlet eyelid: males usually have two spurs with the upper poorly developed. Birds of Mount Kenya (*F. j. pollenorum* Meinertzhagen, 1937) are rather darker than western birds (*F. j. jacksoni*), and in both populations there is individual variation in the extent of white below.

F. nobilis of Ruwenzori and the mountains from Kivu north to Lake Albert is rather smaller than the foregoing species and less patterned than any except the Mega population, *F. c. atrifrons*. It has the head, primaries and tail grey-brown and the mantle and wing-coverts deep maroon, with faint grey scalloping on the upper mantle: the throat is off-white and the rest of the underparts chestnut with some narrow grey or whitish edges or scallops replacing the broad white edges of

jacksoni: there is a conspicuous circle of red skin round the eye: like *F. jacksoni* and *F. castaneicollis* it has a red bill and legs but with the short upper spur of *jacksoni*. The width of the greyish edges to the chestnut feathers below varies individually but, from the limited series available, it seems that in the population of Ruwenzori (*F. n. chapini* Grant & Praed, 1934) they are consistently narrow.

The male of the Cameroon Mountain francolin, *F. camerunensis*, is very like *F. nobilis*, except that the maroon of the mantle and wing-coverts and the grey brown of the back are replaced by a rich dark brown, and the underparts are plain grey with some darker feather centres: the area of bare skin round the eye is more extensive. The female is quite different, being mottled and vermiculated above and below in black, dark brown and buff, with some dark brown or black and off-white U-patterning, on the mantle, breast and abdomen.

The last species of the group is *F. swierstrai* which is found associated with patches of evergreen forest in the Bailundu highlands and along the escarpment in Angola. It is isolated from all other members of the group by over 1,000 miles and, morphologically, is the species least readily linked with any other in the group. Both sexes have conspicuous white eyestripes (not found in other members of the group) and a dull brown mantle and wing coverts, concolorous with the back, but which in the female have irregular blotches and transverse markings of darker and paler brown: the male below is mainly white with the upper breast black contrasting with the white throat, and with the lower breast and abdomen streaked with black on the feather edges: some feathers of the flanks are black with a white U-pattern. The female below is mainly white with irregular black or brown blotches or bars, which are most heavily concentrated on the upper breast to form a mottled band and are sparse in the centre of the abdomen (see Traylor, 1960a: 142). The bill and legs are red or orange red as in most other species of the group but the male has commonly only one spur. It has no red skin round the eye.

EVOLUTION

The distributional pattern presented by these isolated populations associated with high altitude evergreen forest is only readily interpreted if these populations are regarded as relicts from a cold, wet era when the montane forest and the group as a whole had a more or less continuous distribution between the extreme points of which it is now found (Map 3A). Any retreat of the forest would cut off the outlying Cameroon and Angola populations from the eastern birds and they may therefore be presumed to have been isolated for the longest period, allowing greater opportunity for divergence.

Similarly the marked, but less extreme, divergence shown by *F. nobilis*, *F. jacksoni* and *F. castaneicollis kaffanus* is to be expected since the mountains of the Congo border, Kenya and southern Abyssinia are separated from each other by over 300 miles of comparatively low country. In Abyssinia, on the other hand, the problem is more complex for the divergence between the northern *F. erckelii* and the southern *F. castaneicollis* is extreme, yet they are not separated from each other by any greater distance or any greater natural barrier than there is between

the several isolated populations of *F. castaneicollis*. It seems possible that the interpretation of this pattern may be found in the ecological differences between the two species for, from the limited field notes available, it is apparent that *F. erckelii* alone of the Montane Group is not dependent on evergreen forest, being found widely in grassland. (I can find no information on whether it is also found in the evergreen patches within the range, and it is possible that it exploits both habitats.) Furthermore, the unusual degree of uniformity of colour and pattern in *F. erckelii* argues a continuity of range over a long period, so it can be expected that adaptation to this type of habitat, which has a less fragmentary distribution than evergreen forest, took place early in the history of the species soon after it was first isolated by a retreat of the forest. This adaptation would have raised an ecological barrier between proto-*erckelii* and proto-*castaneicollis* which would inhibit interbreeding in any subsequent era in which there was a sufficient spread of evergreen forest to reunite the scattered montane communities in Abyssinia.

It seems unlikely that such a spread has taken place within comparatively recent times, for there has been time enough for divergence between most of the isolated populations of *F. castaneicollis*. This divergence is particularly marked between the populations west and east of the Rift, *F. c. kaffanus* and *F. c. castaneicollis*, and in the isolated Mega population *F. c. atrifrons*, and it is likely that breaks were made earlier between these three groups than between the individual populations of the south-west.

But while *atrifrons* can be regarded without much hesitation as a population which has diverged from *F. castaneicollis*, any guess at the origin of *F. ochropectus* in (French) Somaliland is more doubtful, for it is closest morphologically to *F. erckelii* but has some characters of *F. castaneicollis* and is also a bird of evergreen forest. It could be postulated that, in isolation, it has descended without much variation from the common ancestor of *erckelii* and *castaneicollis*, or that it is a product of hybridisation between them at a later reunion. Although the distances that separate *ochropectus* from the neighbouring species are not great, the country between is so low and dry and it would require extreme climatic change to bridge it with forest or montane grassland, so that the first of these two alternatives seems the more likely.

There is no such formidable barrier between *F. c. erckelii* and the greyer *F. e. pentoni*, isolated in the Red Sea Hills, and the relatively slight divergence between them does not suggest lengthy isolation.

A summary of the evolution postulated is as follows:—

Stage 1. The group widespread in an era in which montane forest covered a large part of Africa (Map 3A).

Stage 2. With a retreat of montane forest proto-*swierstrai* and proto-*camerunensis* become isolated first and subsequently the ancestral stocks of the other species.

Stage 3. In isolation proto-*erckelii* becomes adapted to grasslands.

Stage 4. A limited spread of forest allows interbreeding within the ranges of proto-*nobilis*, proto-*jacksoni* and proto-*castaneicollis*, but though the ranges of proto-*erckelii* and proto-*castaneicollis* may join there is no interbreeding. Proto-*ochropectus* remains isolated.

Stage 5. The forest gradually retreats causing first a split between the populations of proto-*castaneicollis* east and west of the Rift, and isolating the Mega population, proto-*atrifrons*, and next the populations of south-west Abyssinia. Subsequently the forest retreats to its present limits and the country south of the Red Sea Hills becomes unsuitable for *erckelii*, isolating the population at Erkwit.

THE SCALY GROUP (MAP 4)

(*F. ahantensis*, *F. squamatus*, *F. griseostriatus*)

RANGE AND CHARACTERS

The range of the Scaly Group lies entirely within 15° of the Equator, and largely within the limits of the lowland forest in both Upper and Lower Guinea. Inside the forest these francolins are found in clearings and cultivations. Outside the perimeter of the forest there are scattered populations north to the Gambia in the west and to the Jebel Marra in the Sudan, east to Amani in north-eastern Tanganyika, south to the Vipya plateau, northern Nyasaland, and to the Benguela district in Angola. These scattered populations may be found in vestigial patches of lowland forest, riverine forest, montane forest or in cultivations in which there is sufficient cover in which to hide.

The members of the group are the plainest of the francolins, having little defined pattern or strong colour. The upper parts are mostly brown sometimes with underlying vermiculations and with indistinct patterning on the hind neck and mantle, the feathers having paler edges and darker centres varying from blackish to orange-brown. There is no defined pattern on the face and the throat is whitish. The remainder of the underparts are chiefly brown or creamy-buff with the colour and patterning varying in the different forms but all have very narrow darker edges to the breast feathers which give a scaly appearance. The bill is orange or red with some black or brown on the culmen or at the base, and the legs are orange-red, the males having one main spur and commonly a small upper spur in at least two of the three species. There is no marked sexual dimorphism but females tend to be more vermiculated than the males and in some forms tend also to be paler.

SPECIES AND POTENTIAL SPECIES

All forms are allopatric with the three recognised species clearly differentiated, but otherwise geographical variation in most of the range is not well defined and tends to be obscured by individual variation. The West African species (*F. ahantensis*) is found within the limits of the main block of the Upper Guinea forest from Sierra Leone to Ghana and in the part of the Lower Guinea forest lying west of the Niger. Scattered populations are found also in Portuguese Guinea and the Gambia (and might be expected in former French Guinea).

In *ahantensis* the upper parts are indistinctly vermiculated with some white U-patterning on the mantle, the feathers having blackish centres, occasionally with a reddish-brown shaft streak: the underparts are brown with white and darker brown U-patterning: the bill is orange with a black base.

The populations of Portuguese Guinea and the Gambia (*hopkinsoni* Bannerman,

1934) are slightly paler. On the map they appear to be separated from the main body by about 350 miles, but it is likely that scattered populations exist in suitable patches of thick bush along the rivers of (French) Guinea, and that variation will be found to be clinal.

The Niger appears to form a complete barrier between *ahantensis* on the west and *F. squamatus* on the east. The birds found within the boundaries of the forest from the Niger east to the Ituri (*F. s. squamatus*) are the least distinctly patterned of all the group having the upper parts indistinctly vermiculated with faint greyish U-patterning on the upper mantle, the feathers having blackish centres tinged with red-brown: the underparts are plain brown with a scaly pattern and ill-defined darker shaft streaks: the bill is red or orange-red with a darker culmen.

All the scattered populations outside the perimeter of the Guinea forest, namely those from the Sudan, Abyssinia, eastern Kenya, Uganda, western Tanganyika, the southern Congo and north-eastern Angola, are sufficiently alike to be united under the subspecific name *schuetti*. They differ from *F. s. squamatus* in being less vermiculated, with the pattern on the mantle slightly more clearly defined and with more red-brown in the centre of the feathers: below they have a less scaly appearance, the feathers of the abdomen having whitish edges giving an irregular streaky effect. Within this large range there is much individual and some local variation in the amount of white below and in the tone of the browns but no significant geographical variation, although populations are found in varying habitats, in vestigial patches of lowland and gallery forest and in the lower levels of the montane forests of the east Congo (up to about 6,500 ft.), and in the mountains of the southern Sudan (up to 8,500 ft.). In Uganda and Kenya, where much of the forest has been cleared within the last sixty years, *F. squamatus* has become largely adapted to cultivations, but is also found in montane forest up to 9,500 ft. (Mt. Elgon).

West of the Rift in Kenya, southwards to Kilimanjaro, Monduli and Mount Meru in north-eastern Tanganyika, the birds become increasingly darker and greyer, with often less white on the abdomen, especially in the males. The darkest, plainest populations are found on Kilimanjaro (up to 6,500 ft.) (*maranensis*) and in the Chyulu Hills.

Although the range of Scaly Francolins in East Africa is now discontinuous and in these eastern districts the populations are isolated on the mountains (and may be diverging) the variation exhibited appears fundamentally clinal from a time when distribution was continuous. However, only 150 miles south-east of Kilimanjaro birds from the Usambara Mountains (*usambarae*) show a consistent difference, having the lores, eye-stripes and cheeks freckled with black and white instead of being an ill-defined brown. This marking has been described as even more pronounced in a single, rather paler, specimen (the type of *uzungwensis*) from Kigomo, Uzungwe Mountains, in south-western Tanganyika, 350 miles to the south. There are no records of Scaly Francolins from the country between Amani and Kigomo, much of which is totally unsuitable, but it might be expected in forest patches of the Nguru and Uluguru Mountains.

Another isolated population is found still further south on the Vipya plateau of central Nyasaland, in forest between 3,000 and 6,000 ft. (*doni* Benson, 1939), which

is a richer red-brown in the centres of the feathers both above and below, and has very few white streaks on the abdomen; there is some black in the lores and eye-stripe. The colour, but not the extent of the red-brown patterning in the mantle, is matched in a few individuals of *schuetti* from various parts of its range, but none approaches this colour below.

The third species of the Scaly Group, *F. griseostriatus*, is confined to the strip of rich vegetation with vestigial patches of forest which is associated with the escarpment in western Angola. It is the most distinct member of the group having the feathers of the mantle and wing-coverts chestnut broadly edged with grey, and the rest of the upper parts faintly vermiculated, as in *F. s. squamatus* and *F. ahantensis*, but paler: below the feathers of the breast and flanks are chestnut edged greyish or creamy buff and the abdomen is plain creamy buff. While the coloration is brighter and more contrasting, the pattern of the feathers of *griseostriatus* is fundamentally the same as in the other two species. The bill is mainly blackish on the upper mandible with a bright red base, and below is orange-red: the legs are orange-red, and the three males examined have only a single spur.

EVOLUTION

The chief features of the distributional pattern of the Scaly Group are the two specific divisions which separate *ahantensis* and *griseostriatus* from *squamatus*; the vast areas in which *squamatus* exhibits no significant variation: and finally the indications of speciation in the eastern populations. The fact that the ranges of *F. ahantensis*, and *F. s. squamatus* coincide so closely with the limits of the main blocks of lowland forest suggest strongly that glades and clearings in this type of forest must be regarded as the natural habitat for the group, and that the populations found outside the perimeter of the forest are relicts from a period in which the forest extended to the extreme limits of the range of the Group. The occurrence of these populations in montane forest, up to at least 9,500 ft. on some mountains, and the rapid adaptation of the birds in Kenya to cultivations indicate, however, that their requirements are not rigid as long as sufficient cover is available. A wide spread of montane forest might, therefore, not be wholly disastrous for the Scaly Group, though they could not expect to compete entirely successfully with members of the Montane Group in these conditions. (It is perhaps significant that the highest altitudes at which Scaly Francolins have been found are on Mount Elgon, which has apparently no representative of the Montane Group.)

It seems likely, therefore, that prolonged dry eras have been the chief factors in speciation. In some such periods (possibly coincidental) early in the history of the group proto-*ahantensis* could have been isolated from proto-*squamatus* by a belt of savanna stretching to the coast between the Niger and the Volta, and proto-*griseostriatus* isolated along the escarpment of Angola, where moister conditions prevailed, while the interior of the country was dry (Hall, 1960b). With a return of wetter conditions in West Africa proto-*ahantensis* spread eastwards. The lack of divergence between populations on either side of the present gap in the forest east of the Volta lends support to the conclusions cited by Moreau that the gap between

the two blocks of forest was formerly further east in the neighbourhood of the Niger delta. The Niger itself at present lies between the two species, and since there can be little temptation for sedentary birds such as francolins to fly across a broad river it can be regarded as a barrier sufficiently formidable to inhibit interbreeding. It is possible that the Lower Congo could have acted as a similar barrier between *proto-squamatus* and *proto-griseostriatus* if in a wet era the escarpment forests of Angola were reunited with the forest of Gabon and Cabinda.

In *F. squamatus* the remarkable lack of variation in the whole species argues that the last spread of forest which linked the present outlying populations was of comparatively recent date. If degree of divergence can be accepted as a guide to time then it can be postulated that the earliest populations to be isolated by the retreat of the lowland forest would be those of Nyasaland and Tanganyika: but in this instance especially this precept must be posed very tentatively for the isolated populations concerned have also become adapted to rather different conditions at higher altitudes which might accelerate divergence. Since the most geographically remote of the remaining populations, those of the Jebel Marra (known from one specimen only) and southern Abyssinia, do not differ significantly from typical *schuetti* in north-eastern Angola and the southern Congo, the forest may have persisted longest in north-eastern Africa.

Finally the distinction and the fairly sharp transition between *squamatus* and *schuetti* on the perimeter of the Congo forest merits attention. It suggests that at some time western and eastern birds were divided (presumably in a dry era) and on reuniting the eastern birds tended to favour rather more open habitat on the forest fringes, and the western birds clearings in the deep forest.

A summary of the evolution postulated is as follows:—

Stage 1. The group developing in lowland forest, and probably extending to East Africa.

Stage 2. In a dry era *proto-ahantensis* in the Upper Guinea forest becomes cut off from *proto-squamatus* in the Lower Guinea forest somewhere in the region of the Niger. *Proto-griseostriatus* in the escarpment forests of Angola also becomes cut off from *proto-squamatus*.

Stage 3. In a wetter, more favourable, era, the group spreads again but no interbreeding takes place between the incipient species, the barriers formed by the Niger and Lower Congo possibly reinforcing any tendency to genetic isolation that has developed while they have been separated.

Stage 4. A dry era divides the Lower Guinea forest into a western block, in which *proto-squamatus* subsp. develops and an eastern block in which the birds become adapted to slightly less humid conditions. These eastern birds, *proto-schuetti*, keeping more to the forest fringes when the two are reunited.

Stage 5. A wide spread of lowland forest extends the range of *proto-ahantensis* to the Gambia, and *proto-squamatus* sp. to embrace all the outlying localities at which it is found at present (Map 4A).

Stage 6. With the retreat of the forest, populations become isolated first in Nyasaland, *proto-doni*, and Tanganyika, *proto-uzungwensis* and *proto-usambarae*, then on the mountains of the Kenya/Tanganyika border, and finally in the Sudan, Uganda

and Abyssinia. These isolated populations survive in isolated patches of lowland and riverine forest, and also become adapted to montane forest up to high altitudes, especially where there is no competition from members of the Montane Group, and, in some areas, to cultivations.

In West Africa populations of *ahantensis* become isolated in the Gambia and Portuguese Guinea and the main block of the species is divided by a break in the forest in the region of the Volta.

THE VERMICULATED GROUP (MAP 5)

(*F. bicalcaratus*, *F. icterorhynchus*, *F. clappertoni*, *F. hildebrandti*, *F. natalensis*, *F. hartlaubi*, *F. harwoodi*, *F. adspersus*, *F. capensis*)

RANGE AND CHARACTERS

The Vermiculated Group is the most widespread of all the African groups. I regard it as consisting of a superspecies (containing six allopatric species) and three related species. The superspecies has a more or less continuous distribution from Senegal to Eritrea and southwards to Natal with outlying populations in Morocco and in the mountains of South West Africa and southern Angola. Of the three extraneous species one (*F. harwoodi*) is confined to a small area of Abyssinia almost encircled by the superspecies: the second (*F. adspersus*) replaces the superspecies in northern Bechuanaland but is partly sympatric with the outlying population in South West Africa: the third (*F. capensis*) is completely isolated in the extreme south.

The ecology of the group is variable and will be discussed in detail under the individual species but it can be said in general that from West Africa to Abyssinia and Uganda the members of the superspecies (*F. bicalcaratus*, *icterorhynchus* and *clappertoni*) are birds of grasslands and cultivations in the woodland, acacia savanna and steppe belts. However, in east and southern Africa this habitat is largely occupied by members of other groups, in particular *F. afer* of the Bare-throated Group (Chapin 1932: 714), and it appears that members of the Vermiculated Group have been driven into more rocky country on hillsides and into thickets in river valleys and the distribution is consequently more broken (compare Maps 2 and 5).

In choosing the term "vermiculated" as the descriptive name for this group I have given emphasis to the most striking character which the majority of the component forms have in common although in some subspecies of *F. clappertoni* the vermiculations are largely or wholly replaced by extensive U-patterning. All members have brown or grey-brown heads, backs, wings and tail, with lighter vermiculations and/or V- and U-patterning, and sometimes some rufous mottling: the lores are black or blackish and most forms have a white eye-stripe: the underparts are patterned with dark brown (and sometimes chestnut or maroon) on a whitish or cream background, except in the females of the two sexually dimorphic forms which are plain orange-ochre below: the colours of the bill and legs, and the colour and extent of bare facial skin, is variable and so is the number of spurs (see Table 1).

SPECIES AND POTENTIAL SPECIES

The superspecies consists of six clearly differentiated forms which are usually regarded as species, though it can be argued that two of these, *F. hildebrandti* and *F. natalensis*, could be treated as conspecific. The three northern members, *F. bicalcaratus*, *F. icterorhynchus* and *F. clappertoni*, form a homogeneous assemblage occupying grasslands and savannas of various types. *F. bicalcaratus* is the representative in West Africa, being common in the acacia and woodland belts from Senegal to the Cameroons, extending also into cleared parts of the Upper Guinea forest. There is also an isolated population in Morocco. Above, it is faintly vermiculated with extensive V- or U-patterning on the mantle and wing-coverts: below, each feather is cream with some chestnut on the edges and with a black drop-shaped centre that is broken by small cream "windows" (Fig. 1, 15), giving a partly streaked and partly spotted effect: the bill and legs are greenish, and two fairly well-developed spurs are common in the males.

The Morocco population (*ayasha*) is not conspicuously different, though isolated by 1,500 miles, but may be slightly more rufous and with rather smaller "windows" in the patterning below. Other variation in the species is clinal and will be discussed later.

In the Cameroons, at about longitude 15°E., *F. bicalcaratus* is replaced abruptly (but not apparently along any ecological boundary) by a plainer bird, *F. icterorhynchus*, which is more vermiculated and less V-patterned above, and which is irregularly V-patterned, blotched or spotted with dark brown below: the bill and legs differ from *bicalcaratus* in being mainly orange, and there is a small patch of yellow skin round the eye. Its range extends eastwards through the woodland belt (Map 11, types 16 and 17) to Uganda, where a few specimens are found which have some chestnut streaks on the flanks (as in the type of "*F. ugandensis*"). In the acacia belt to the north (Map 11, type 20) *F. clappertoni* replaces *F. bicalcaratus* between northern Nigeria and Lake Chad, and replaces *F. icterorhynchus* in the Sudan. It is common also in the Nile and Blue Nile valleys and on grassy hillsides of western Abyssinia and Eritrea below 7,000 ft. (above which it is replaced by the montane francolin, *F. erckelii*). Western birds (*F. c. clappertoni*) are very similar to *F. icterorhynchus* above but a more orange brown, while below they resemble *F. bicalcaratus* except that there are no "windows" in the dark feather centres and the feathers are edged with maroon rather than chestnut. In the Nile valley and southern Sudan birds become darker and greyer, less vermiculated, but heavily U-patterned above and more heavily patterned below on a whiter ground. In the Blue Nile valley and eastwards birds lack vermiculations entirely but are clearly and regularly V-patterned above and on the breast, giving a lanceolate appearance, and they lack the moustachial streak which is present in the western birds.

A single specimen collected at "Ngeem", Lake Chad (possibly Nguigmi on the north-west edge of Lake Chad), the type of "*F. tschadensis*", is very like some of the specimens of *F. clappertoni* from the Nile valley but the underparts are more buffy and lack any maroon markings, and it is rather less heavily patterned on the back. Neumann suggested (*cf* Bannerman, 1: 327) that it is a hybrid between *F. clappertoni* and *F. icterorhynchus*. Since *F. icterorhynchus* does not now apparently occur as

far north as this, and since this specimen is rather more heavily patterned than the northern populations of *icterorhynchus* and *clappertoni* it might perhaps be better regarded as an aberrant specimen that indicates the close relationship of the two species.

East and south of Lake Victoria *F. icterorhynchus* is replaced by *F. hildebrandti*, which is a bird largely associated with rocky ground and thickets in river valleys and on hillsides, from sea level to about 8,000 ft., and which is found equally in the acacia savanna and the brachystegia woodland belts. It is common from central Kenya south to the Tabora and Dodoma districts of Tanganyika but in the southern part of Tanganyika and northern Mozambique its distribution is sporadic: however, it is again common in Nyasaland at varying altitudes, and in the upper Luangwa valley. The males are very like *F. icterorhynchus* above, but have more solid, blotchy, brown markings below: the bill is reddish with a brown culmen and yellowish base, and the legs reddish. The female is quite different having the underparts plain orange ochre. The sexual differences are most complete in the most southerly birds from southern Nyasaland, Mozambique and south-west Tanganyika (*F. h. johnstoni*) in which the female has no patterned plumage on either the upper mantle or the breast, whereas those from most of Kenya (*F. h. altumi*) have some patterned "male" plumage on both. Females from the centre of the range (*F. h. hildebrandti*) are intermediate, having the patterned feathers mostly confined to the upper mantle.

F. hildebrandti reaches the southern limits of its range in the Luangwa and Shiré valleys, and is replaced further south by *F. natalensis*, a bird with apparently the same ecological preferences. Birds from the Transvaal and Natal and the southern parts of Southern Rhodesia (*F. n. natalensis*) differ from *hildebrandti* in having the sexes alike, the backs darker brown and more heavily patterned and vermiculated and having regular double U-patterning below, unlike the brown blotches of the male *hildebrandti*. The bill and legs of *natalensis* are similar to those of *hildebrandti* except that there is no black on the culmen and the male has commonly one spur and the female none, whereas in *hildebrandti* the male has commonly two (once three) spurs and the female one or two vestigial spurs. However, the intensity and regularity of the patterning, particularly in the females, decreases northwards, showing some approach to *hildebrandti*. The populations of the northern districts of Southern Rhodesia, the Zambezi valley and the Luangwa valley (*neavei*) are plainer and more rufous above and the females tend to have the underparts washed with buff, the abdomen plainer and the U-patterning less defined giving a more spotted or streaked effect, but there is much individual variation.

As far as is known the ranges of *F. hildebrandti* and *F. natalensis* only approach each other in two areas, in the Luangwa valley between latitudes 12° and 13°S and in the neighbourhood of the Shiré/Zambezi confluence. In the Luangwa valley there is some indication that the two may sometimes interbreed, or have interbred in the recent past, for some of the specimens of *natalensis* are more blotched, less U-patterned below than those of *F. n. neavei*, and some of the females are washed with buff below and have plainer abdomens (see Benson and White, 1957: 138): one male from Jumbe (13° 16'S., 32° 07'E.) lent by the National Museum of

Southern Rhodesia is close to *F. n. neavei* below but has, like *hildebrandti*, a dusky ridge to the culmen and two spurs. Nevertheless, there are in this area specimens typical of the two forms taken from within 50 miles of each other so it is probable that there is only sporadic interbreeding.

In the Zambezi/Shiré area the situation seems rather different. *F. natalensis* has been collected from points along the Zambezi as far down as Tambara (60 miles below Tete) but not as low as the junction with the Shiré, and not from the left bank below the junction of the Mushonganende River, 280 miles above Tete. Within 40–60 miles of Tambara *F. hildebrandti* has been collected in southern Nyasaland and neighbouring Mozambique at Zobue, "on rocky hillsides" (Vincent 1934: 336), on Mlunganyama hill "at 500 ft. but not at 200 ft." (Benson, C. W. & F. M., 1948: 3), on Mwananbidzi Hill at 2,500 ft., and near Port Herald in the Shiré valley (Long, 1960: 100), but not as far down the Shiré as the confluence. There is no evidence in this area of interbreeding between *F. natalensis neavei* and *F. hildebrandti* and it has been suggested that here the Zambezi itself, which is as much as two miles wide when in flood, may be a barrier (Benson, *et alia*: in press).

The last member of the superspecies, *F. hartlaubi*, is confined to the mountains of northern South West Africa and southern Angola and is strictly a bird of the rocks. It is the smallest member of the group and has distinctive rufous mottling above. The females are rufous below like those of *F. hildebrandti* but the male is finely streaked from chin to abdomen in brown and white. The bill is brownish above and yellow below and at the base: the legs are yellow with spurs poorly developed but often with two present vestigially in both sexes.

The first of the three members of the group which are not included in the superspecies is a francolin about which little is known, *F. harwoodi*. Only males have been collected and from only three localities, all in the gorges of the Upper Blue Nile or its tributaries. Of members of the superspecies it resembles *F. natalensis* most closely, being similar above but with more defined U-patterning on the nape, and below having similar double U-patterning, but rather darker and more clearly defined and extending to the chin, and being absent from the centre of the abdomen, which is cream. It is distinctive in lacking the white eye-stripe but having a circle of bare scarlet skin round the eye. The bill is recorded as red but from the appearance of skins probably has a black culmen; the legs are red with two fairly well-developed spurs. *F. harwoodi* appears to be cut off from other members of the group by the presence of the montane francolin *F. erckelii* on the plateau above the gorges, in the type of open country which, at lower altitudes, is occupied by *F. clappertoni* both to the north and the south.

In southern Africa along the borders of Rhodesia and Bechuanaland the superspecies (represented by *F. natalensis*) is replaced in similar habitat by *F. adspersus*, which ranges westwards through both acacia savanna and steppe (Map 11, types 20 and 25) to South West Africa where it overlaps the range of the isolated member of the superspecies, *F. hartlaubi*. Here the two forms are found in the same localities but differ in their ecology and habits, *adspersus* living in coveys along watercourses and *hartlaubi* usually in pairs on the rocks. *F. adspersus* is a rather different-looking bird from those members of the group that have been discussed: its appearance is

grey, the pattern being composed of minute vermiculations on the upper parts and with broader black-and-white vermiculations over all the underparts. It has no eyestripe but an area of bare yellow skin round the eye: the bill and legs are orange-red, the male having usually a single long spur.

The last member of the Vermiculated Group, *F. capensis*, is isolated in the extreme south-west. Like many other members of the group it is found in thick cover in rocky river valleys chiefly in the coastal districts of the Cape. It is not known from Little Namaqualand (possibly because of the lack of suitable rivers) but has been recorded from the gorge of the lower Orange River at Assenkjer. It is the largest member of the group and most like *F. natalensis* and *F. harwoodi* in the predominance of brown and white double U- or double V-patterning. However, in *capensis* the patterning is distinctive in being composed of very fine irregular white lines on most of the back (the rest being vermiculated), and similar on the underparts but with distinct white shaft streaks, giving a streaky effect: it has no eye-stripe and no bare skin round the eye: the bill, as in *hildebrandti*, is red with a dark culmen, and the legs red, the male having one or two spurs and the female one.

OTHER VARIATION

In *F. bicalcaratus* variation is largely clinal, the palest birds being found in the drier savanna areas and the darkest and most heavily patterned in the cleared parts of the forest areas in southern Cameroons. Among the dry country birds those from Senegal, Gambia and the hinterland of Ghana (*bicalcaratus*) are paler with more rufous heads than those of northern Nigeria and northern Cameroons (*adamauae*). The birds from within the borders of the Upper Guinea forest from Sierra Leone to Ashanti (*thornei*) are slightly whiter, less creamy below than those within the borders of the Lower Guinea forest from south-eastern Nigeria and southern Cameroons (*ogilviegranti*) which become increasingly dark eastwards. Birds from Accra, between the two forest blocks, are closer to *bicalcaratus* than to *thornei*: those of most of southern Nigeria are intermediate between *adamauae* and *ogilviegranti*. The isolated *ayesha* in Morocco (already discussed) is closest to the paler birds above but has heavier patterning below.

In *F. icterorhynchus* variation is clinal and ecological, pale, lightly patterned birds being found in the southern Sudan and in the region of the Albert Nile in northern Uganda (*icterorhynchus*): dark, heavily patterned birds are found in the more humid areas from the Oubangi and Uelle to southern Uganda (*dybowskii*).

In *F. clappertoni* the clinal variation is greater than in the two previous species, and features some changes in pattern that warranted discussion in the main section. West of the Nile and in the Nile Valley the paler, less patterned *clappertoni* merges through the intermediate *heuglini* to the dark U-patterned *gedgii* of the southern Sudan. Among the more V-patterned, lanceolated populations of the east, those of Eritrea, and northern Abyssinia (*sharpii*) are pale above (though not as sandy as *clappertoni*), those of south-western Abyssinia (*nigrosquamatus*) are darker and more patterned, and those of the Blue Nile valley (*konigseggi*) are somewhat intermediate, closest to *sharpii* but with a greater suffusion of black markings below.

In the southern populations of *F. natalensis* there is some variation according to the habitat, darker, more patterned birds being found in the richer vegetation of Natal, Zululand, and the Zoutspansberg, and paler birds in the drier savanna country of the Transvaal (see Clancey, 1953: 59). (Since the range of the darker birds is discontinuous it is impracticable to distinguish the two variations by name.)

The available series of *F. hartlaubi* is inadequate for detailed study, but it would seem that the populations of southern Angola (*hartlaubi*) are rather smaller than those of South West

Africa, and that the western birds from the Kaokoveld and Erongo (*crypticus* Stresemann, 1939) are rather paler than those from the Waterburg and Otavi further east (*bradfieldi*).

EVOLUTION

It has already been suggested that the rather different ecology of the northern members of the Vermiculated Group compared with those from Kenya southwards may be due to competition with the Bare-throated Group, and this possibility has considerable bearing on the interpretation of the pattern presented by the ranges of the various species. I believe, for example, that while the present can be regarded as generally favourable for the Vermiculated Group as a whole, it is even more favourable for the Bare-throated Group and that the distribution of the southern vermiculated species is heavily restricted because of this, especially in the areas where alternative habitats to the savanna grasslands are limited.

This would account for the absence of any member of the group from the grasslands south of the Congo forest, also for the sporadic distribution in eastern Africa, and possibly also for the limited ranges of *F. natalensis* and *F. capensis* in the coastal districts of the south-east, where the gap between them is occupied by the bare-throated *F. afer*.

In the north-east it is apparent from the isolated population in Morocco that the group is not at present as widespread as it has been at some time in the not distant past (to judge by the lack of divergence in the Morocco population). Elsewhere in the north the range appears to be expanding, for there is good reason to suppose that *F. clappertoni* has only recently extended its range in the acacia savanna south of the Sahara, where it has supplanted *F. coqui* (see discussion under Red-tailed Group and Maps 5 & 8), and also has recently extended its range eastwards towards the Red Sea coast, cutting off the Erkowit population of the montane francolin (*F. e. pentoni*) from the main body of the species (compare maps 3 and 5).

From the foregoing it can be assumed that grasslands and scrub in savanna and woodland are the natural habitat for the group, but it is adaptable: the presence of several members in areas where the rainfall is under 10 inches a year shows especially that it can be tolerant of dry conditions if there is adequate cover in watercourses. It is likely, therefore, that humid eras in which there has been a wide spread of forest have been less favourable to the group than the dry eras, and that it is chiefly in these wet eras that the group has been split and speciation has developed in the isolated populations. The morphological differences between *F. adspersus* and other members of the group, combined with the fact that it has diverged sufficiently to be able to live alongside another member, *F. hartlaubi*, in complete ecological segregation, suggest that probably the group developed in the east and south-east and that proto-*adspersus* was isolated earliest from the original stock. This could conceivably have taken place at the time when a spread of montane forest linked the Natal forests with those of Southern Rhodesia and Nyasaland, cutting off proto-*adspersus* in the Kalahari/South West African region. Proto-*capensis* and proto-*harwoodi* can be presumed also to have been isolated at an earlier period than any of the six members of the superspecies, but several factors could have caused their segregation. Proto-*capensis*, as suggested, could have been cut off by the

intrusion of the bare-throated *F. afer*. *F. harwoodi* on the other hand appears to be a "relict" population that has survived in the Blue Nile Gorges at a period when the group was overrun on the plateau above. The fact that the high parts of the plateau immediately surrounding the range of *harwoodi* are at present occupied by *F. erckelii* of the montane group suggests that it was first split from other members of the group in an era when montane conditions prevailed all over the plateau, as they do now.

Proto-*hartlaubi* in South West Africa may also have been cut off at an early date from the remainder of the superspecies, in which case it must be regarded as a coincidence that it has diverged along the same very distinctive lines (with marked sexual dimorphism) as the Tanganyika population, *hildebrandti*. It seems more likely that, following the periods in which *adspersus*, *capensis* and *harwoodi* were isolated, there was a period which favoured the superspecies, during which it became widespread through the grasslands of the tropics and south to Natal and the Transvaal. Meanwhile, proto-*adspersus* had become adapted to rather drier conditions in acacia steppe to the south-west. A subsequent drier era in southern Africa which spread acacia steppe through the Limpopo and Zambezi valleys could isolate proto-*natalensis* from the rest of the superspecies at a time when proto-*hartlaubi* and proto-*hildebrandti* were still linked. A further spread of steppe northwards bringing competition with proto-*adspersus* or a spread of the Bare-throated Group might then eliminate the superspecies from the areas between the Rhodesias and South West Africa, where there is little alternative habitat. The mountains of the west, however, would provide sufficient ecological variety for proto-*hartlaubi* to find a different habitat and co-exist in South West Africa with proto-*adspersus*, and in southern Angola with the bare-throated *afer*.

The tendency to approach *hildebrandti* shown by the Zambezi population of *natalensis* (*neavei*) suggests that these birds are either closest to the ancestral stock of *natalensis*/*hildebrandti* or else are the result of a period in which the two had become reunited after their distinctive characteristics had developed, but before there was any bar to free interbreeding. However, the lack at present of an intermediate population showing all stages of intergradation between *hildebrandti* and *natalensis* suggests that the ranges of the two were again separated in the not too distant past: the presence in the Luangwa valley of a few apparent hybrids among otherwise typical birds indicates that there has been only sporadic interbreeding now that the ranges again join. Minor fluctuations in climate would serve to bring about this splitting and reuniting.

The differences between the various populations of *hildebrandti* are not great enough to suggest any lengthy periods of isolation, but, combined with the present discontinuous distribution, indicate a limited amount of splitting and reuniting since the species developed. The greater amount of "male" plumage exhibited by the females of *hildebrandti* in western Kenya (*altumi*) indicates some approach to *F. icterorhynchus* of Uganda, suggesting that the break between them was at a comparatively recent date.

The three northern members of the superspecies, *icterorhynchus*, *clappertoni* and *bicalcaratus* form a homogeneous and completely allopatric assemblage from which

it can be postulated that the present extensive range has not been occupied for a long period, since otherwise climatic fluctuations would have caused complex splitting and rejoining of populations over such a wide area. To interpret the main lines of the pattern it is only necessary to visualise one period in which the ancestral stock of the three members spread westwards from Abyssinia to Senegal, followed by one unfavourable period in which it was divided into a western (proto-*bicalcaratus*), central (proto-*icterorhynchus*), and eastern (proto-*clappertoni*) population. This period seems likely to have been a humid one in which Lake Chad was extensive and forest extended from its southern tip southwards, forming a north-south barrier between the western and central parts of the savanna belt. At the same time it can be postulated that there would have been sufficient riverine forest along the Nile to form a second barrier further east, and that forest in Kenya and Uganda cut off proto-*icterorhynchus* from proto-*hildebrandti* in the south. Speciation developed in the three pockets and was almost complete when dry conditions returned. Proto-*clappertoni* became adapted to rather drier conditions than the other two species and spread eastwards over the Nile north of proto-*icterorhynchus*. The differences in pattern between the eastern and western populations of *clappertoni* suggest that at some subsequent period the Nile and its tributaries again formed a barrier between east and west, allowing birds with the distinctive V-patterning of *F. c. sharpii* to develop in the north-east. At present it appears that *clappertoni* is extending its range westwards, north of the ranges of *icterorhynchus* and *bicalcaratus*, at the expense of the red-tailed *coqui*.

In the west it is apparent that there must have been a period when sufficiently humid conditions prevailed along the coast to allow the francolins to spread to Morocco. The lack of marked divergence in the Morocco population (*ayesha*) suggests that this period was of a more recent date than the humid period postulated for the isolation of the ancestral stocks of the three northern species.

A summary of the evolution postulated is as follows:—

- Stage 1.* Ancestral stock of the group develops in the east and south-east.
- Stage 2.* Proto-*adspersus* isolated in the south, possibly by a spread of montane forest.
- Stage 3.* The rest of the group extends northwards to Abyssinia, and widely through grasslands south of the Congo. Proto-*capensis* isolated, perhaps by competition with the Bare-throated Group.
- Stage 4.* The group spreads westwards to Senegal but withdraws from the high plateau of Abyssinia, which is occupied by the Montane Group, leaving a relict population in the Blue Nile gorges, proto-*harwoodi*.
- Stage 5.* (South). Proto-*natalensis* isolated, possibly by extension of acacia steppe in Limpopo or Zambezi valleys bringing competition with proto-*adspersus*.
- Stage 5.* (North). Proto-*bicalcaratus* in the west, proto-*icterorhynchus* in the centre and proto-*clappertoni* in the east, isolated from each other, probably by a belt of forest extending northwards to Lake Chad (at a time when its area was more extensive), and by riverine forest in the Nile valley. Proto-*clappertoni* becoming adapted

to drier conditions than the other two species. Forest in Uganda and Kenya separates proto-*hildebrandti* from proto-*icterorhynchus*.

Stage 6. (South). Proto-*hartlaubi* isolated in the mountains of South West Africa and Angola, possibly by an invasion of the central areas by proto-*adspersus* or by the Bare-throated Group.

Stage 6. (North). Minor fluctuations, allowing proto-*clappertoni* first to spread westwards across the Nile and then splitting into a western and eastern population, possibly during a return of more humid conditions when the Nile valley again became a barrier.

Stage 7. (South). Minor fluctuations causing rejoining and re-splitting of proto-*natalensis* and proto-*hildebrandti*, and isolating populations of *hildebrandti* for short periods.

Stage 7. (North). A humid period in which proto-*bicalcaratus* spreads to Morocco, followed by a drier period in which the Morocco population is isolated.

Stage 8. (South). The ranges of *natalensis* and *hildebrandti* rejoin, at least in the Luangwa valley, and there is sporadic interbreeding.

Stage 8. (North). In the Sudan *clappertoni* spreads westwards through the drier acacia belt.

THE STRIATED GROUP (MAP 6)

(*F. sephaena*, *F. streptophorus*)

RANGE AND CHARACTERS

The Striated Group is unlike all others in consisting of only two species which are partly sympatric. The range of the group as a whole is mainly in eastern Africa, from Somalia to Natal, but extending across to South West Africa and southern Angola, and with an isolated population in the Cameroons.

Both species are mainly brown above with some chestnut, black and white pattern in the collar, and white shaft streaks on the mantle: the eye-stripes are white, edged with black and there is some chestnut on the sides of the face: the throat is white bordered with chestnut: the underparts are creamy buff with contrasting maroon, chestnut, or black-and-white patterning on the breast (different in the two species) and lighter patterning on the flanks and abdomen.

The habitat of the two species is different and will be discussed later.

SPECIES AND POTENTIAL SPECIES

The two species are quite distinct both ecologically and morphologically. *F. streptophorus* has a puzzling distribution, being found commonly in the grasslands and "orchard bush" of northern Uganda and sporadically in north-western Kenya usually on stony scrub-covered hillsides (Jackson, 1938: 241). In north-western Tanganyika Dillingham has found it also in clearings of brachystegia. These are the only areas from which it is known in the east but 1,500 miles to the west a single specimen was obtained by Bates among grass and rocks between 3,500 and 4,000 ft.,

in the Cameroon highlands 40 miles west of Fumban (on the borders of former British and French Cameroons).

It is a darker bird than *F. sephaena* the back being grey-brown with dark brown patches and with fewer and narrower white shaft-streaks. It has a solid chestnut collar on the hind neck above a broken black-and-white collar of barred feathers: there is a considerable amount of chestnut in the facial pattern but only a narrow band bordering the base of the throat: the feathers of the breast are barred black and white occasionally with a chestnut tip: the remainder of the underparts is pale cream marked with some dusky vermiculations and broad blackish streaks on the flanks: the bill is black with yellow at the base and the legs yellowish with only a vestigial spur in the males. The sexes are alike. The Cameroon bird is like those of East Africa but smaller (wing ♂ 145 against 6♂ 151-160).

In northern Uganda, where both species are found, Pitman tells me that *sephaena* is strictly confined to the driest areas of scrubby thorn country while *streptophorus* is in savanna grasslands. Both Jackson (1938: 241) and Dillingham (*in litt.*) stress that the call of *streptophorus* is quite unlike that of any other francolin known to them, and is a melodious trill or whistle. Dillingham on the other hand found *sephaena's* call closer to other francolins though Vincent, on a label of a bird from Swaziland, describes it as "a loud piping trill" and Benson tells me he has found it very variable, Rhodesian birds being hardly recognisable as the same species as those in Abyssinia. Comparison between the eggs would also be useful for Pitman confirms Jackson's statement that the eggs of *sephaena* are exceptionally hard, and it would be interesting to know if those of *streptophorus*, at present unknown, have the same character.

F. sephaena is widespread in the acacia savanna and steppe from eastern Abyssinia and (British) Somaliland westwards to the Albert Nile, southwards through Kenya and along the Tankanyika coast to Mozambique and Natal, westwards to South West Africa and southern Angola. It is never far from water and in the driest parts of the range is confined to watercourses.

Above it is a rich red-brown with broad white shaft-streaks: the chestnut collar is broken with white and the patterned feathers of the upper mantle are rich dark brown or blackish with elliptical white centres: the females are slightly vermiculated. There is no black on the underparts, the feathers of the breast being cream with triangular chestnut or maroon markings on the tips: the bill is wholly black and the legs carmine, the males having a single long sharp spur.

The birds here designated as *F. sephaena* have sometimes been considered to belong to two species, for two distinct types are found, one, mainly coastal, which has fine, drop-shaped maroon streaks on the abdomen, and the other in which the abdomen may have some dusky patterning but which has no maroon streaks. In the Shiré valley of southern Nyasaland birds of the two types appear to behave as species being found close to each other without an ecological division, but without any intergrading: specimens from the southern tip of Lake Nyasa and eastwards are streaked, and so are those from the lower Shiré valley at Chiromo and Tangadzi, but a specimen from Lengwe, 35 miles upstream, is unstreaked, as are those from all localities westwards in the Zambezi valley (Benson, C. W. and F. M., 1948: 3).

In northern Tanganyika a similar clear division is found between the two types, birds from inland, at altitudes above 1,500 ft., being unstreaked, those from the coastal plain being streaked. However, from the Kenya boundary northwards there is no clear division either geographically or morphologically: in western Kenya, southern Abyssinia (Benson, 1945: 391) and throughout Somalia both types are found, as well as some intermediates with sparse, fine streaks. In (British) Somaliland streaked birds predominate at lower altitudes near the coast but both types are found in the highlands and streaked specimens have been found as far inland as Harar in north-eastern Abyssinia. There is no evidence that the two types behave here as species and it is more probable that they represent a hybrid population. (For this population it is convenient to use the name *spilogaster*, which was given to a streaked bird from Harar—see Rand, 1950: 384 while *rovuma* should be confined to the unmixed streaked populations from Tanganyika southwards.)

It will be seen from the map that inland birds of the unstreaked type are found in two blocks from northern Tanganyika northwards and from southern Nyasaland southwards, the species being absent from inland areas through most of Tanganyika, Nyasaland and Northern Rhodesia. Birds of the northern block (*grantii*) have the patterning on the collar and on the breast more restricted (especially in the females) than the southern birds. In birds of the southern block the patterning on the collar is brighter and more extensive and the patterning below extends to the lower breast: birds from the Transvaal, Natal and extreme southern Mozambique (Coguno) have the rest of the underparts fairly heavily vermiculated (*sephaena*), but northwards through Southern Rhodesia the vermiculations become lighter and birds from South West Africa and southern Angola across the continent to southern Nyasaland are appreciably less patterned (*zambesiae*).

OTHER VARIATION

Throughout the range of *F. sephaena* there is considerable local variation in size with equatorial birds on the whole being smaller. Exceptionally small birds are found on the Kenya coast and exceptionally large ones in the Upper Zambezi and Chobe valleys. Among birds without the chestnut streaks on the abdomen there is considerable variation in the amount of vestigial patterning on the abdomen, some having ill-defined whitish streaks and irregular dusky U-patterning. On the whole eastern birds in, and bordering, the hybrid zone tend to be more patterned than western.

In South West Africa some rather greyer birds are found, probably associated with the limestone pans, but the variation is not constant.

EVOLUTION

The peculiar distribution of *F. streptophorus* is the major problem set by the Striated Group. The fact that the eastern and western populations of *streptophorus* are not strongly differentiated and yet the country in between appears totally unsuitable for the species indicates that these are relicts from an era when the group had a wide distribution north of the Congo forest. Being relicts they may not now be in their natural habitat and it can, therefore, be reasonably postulated from the distribution of *sephaena*, that the natural habitat of the Group is in acacia steppe, and that proto-*streptophorus* once occupied this belt from the Sudan westwards,

north of the forest and woodland belts. One thinks usually of these belts as moving north and south with successive climatic fluctuations, but it is possible to visualise that the ridge of higher ground that stretches at about latitude 6°N from the Cameroons eastwards to Uganda may sometimes dislocate regular north-south movement. It seems possible that, following a dry era in which the belt of acacia steppe lay as far south as this ridge, the return of more humid conditions and richer vegetation might come first to the lower country of the Shari basin and Bahr-el-Ghazal to the north of the ridge, leaving temporarily a pocket of dry country on the ridge while the main belts moved north. If proto-*streptophorus* became isolated in this pocket it could be expected that, as conditions became more humid and less and less suitable, it would be driven to the only parts where a tolerably dry habitat could still be found, and one which would be unattractive to the indigenous francolins of the encroaching woodlands. Such refuges were provided in the higher ground at the western and eastern extremes of the previous range.

It is possible that *streptophorus* may yet be found in the country between the Cameroons and Uganda, but if so could be expected only in some patches of sparse vegetation. Since so little divergence is shown by the Cameroon bird it can be postulated that it has been separated from the Uganda population at a comparatively recent date.

The pattern presented by *sephaena* points to at least one unfavourable era in which the species was divided for long enough to allow the streaked and unstreaked types to develop in isolation, almost to the specific level. The present distribution shows how small an extension of woodland towards the coast in Tanganyika would divide the species. In a considerably wetter era with a wide spread of woodland or forest it is likely that the northern populations would be confined to the coastal plain of Somalia while the southern populations might develop on the fringes of the Kalahari. If this was followed by a dry era with a spread of acacia the unstreaked southern populations might spread northwards up the Luangwa valley, through Tanganyika and Kenya along the valleys of the rivers which run westwards to the lakes, and then up the Abyssinian Rift to the Somali highlands.

Meanwhile the streaked northern populations spread southwards, chiefly in the valleys of the rivers flowing to the sea. It is difficult to account for the fact that the two types seem to behave as species in the south but mix and interbreed to a limited extent in the north. It may be that the two came together at a later date in the south when speciation was further advanced, and it is also possible that in northern Tanganyika the sharper change of altitude on the edge of the coastal plain may provide here a barrier that is lacking in Kenya and eastern Somalia (though not in the mountains of (British) Somaliland).

The present gap in distribution between the unstreaked birds of Kenya and northern Tanganyika (*grantii*) and those of the Rhodesias and southern Nyasaland (*zambesiae*) is sufficient to account for the divergence between them.

The scattered distribution of *sephaena* along watercourses in the drier areas would account for much of the local variation in both size and patterning that is exhibited, for such populations would be isolated and might be expected to diverge in periods when there is little suitable vegetation between one river valley and another.

A summary of the evolution postulated is as follows:—

Stage 1. Ancestral stock occupying the acacia belt north, east and south of the central forest and woodland block.

Stage 2. The stock split into two, one, *proto-streptophorus*, in the acacia belt north of the central forest, the other, *proto-sephaena*, in acacia in the eastern districts from Somalia to southern Africa. This split probably taking place in a humid era with a spread of woodland or forest between Uganda and Abyssinia.

Stage 3. *F. sephaena* split into a northern group, probably confined to lowland in Somalia, and a southern group, probably on the borders of the Kalahari. The northern group being the ancestral stock of the birds with streaked abdomens, and the southern group of those with unstreaked abdomens. This split taking place in an even wetter era than Stage 2 with a wide spread of forest and woodland over most of central Africa. *Proto-streptophorus* still isolated south of the Sahara.

Stage 4. (East). A return of arid conditions with increased acacia allows the northern streaked birds to spread down the coast, and the southern, unstreaked birds to spread north up the Luangwa valley, through western Tanganyika and Kenya and the Abyssinian Rift. The two types meet first in the north, and in Somalia they mix and interbreed to a limited extent forming a hybrid zone but with streaked birds always predominant near the coast. Subsequently they meet in northern Tanganyika and later still in southern Nyasaland, but do not interbreed.

Stage 4. (North). In a dry era the acacia belt and *proto-streptophorus* move south to the ridge of high ground from the Cameroons to Uganda and north-western Kenya (Map 6A).

Stage 5. (East). An increase in humidity with a spread of woodland in central Africa cuts off the northern unstreaked birds, *proto-grantii* subsp., from the southern unstreaked birds, *proto-zambesiae/sephaena* subsp.

Stage 5. (North). An increase in humidity, coming first to the low ground of the Shari basin and Bahr-el-Ghazal, north of the ridge, isolates *proto-streptophorus* along the ridge. Increased humidity and competition with indigenous woodland species drive it into refuges at the extremes of its range where more arid conditions persist.

THE RED-WINGED GROUP (MAP 7)

(*F. psilolaemus*, *F. shelleyi*, *F. africanus*,¹ *F. levaillantoides*, *F. levaillantii*, *F. finschi*)

RANGE AND CHARACTERS

This is a very homogeneous group which ranges over most of eastern and southern Africa from Eritrea to the Cape and westwards to Angola. The various species have a complex distribution but are largely allopatric though the ranges of three overlap in the Transvaal. Members of the group are found in a wide variety of habitat and at any altitude, and even individual species are found in varying habitats in different parts of their range.

¹ *F. afer* of Praed & Grant—see appendix.

All birds of the group have "quail-type" plumage on the backs, with a lattice-work pattern of irregular white or buff bars and shaft streaks on a basic colour of mixed black, brown, grey and chestnut: all have the under wing-coverts and part of the wing chestnut (including the South African form *F. africanus*, commonly known as the Greywing, in which the chestnut is reduced): all have a marked facial pattern but this, and the pattern on the underparts, varies in the different forms: all have black bills, usually with a yellowish base, and yellowish legs, the males usually with a single spur. The sexes are alike.

SPECIES AND POTENTIAL SPECIES

The distribution and relationships of the various forms of this group would be easier to discuss if no previous attempt had been made to designate species or subspecies in the East African forms. I cannot agree with any of the classifications made for this group which seem to place too great a reliance on minor morphological characters, particularly the size of the bill, without regard to the ecology of the forms of their likely evolution. The rearrangement I propose I believe to be more realistic in these respects, though I appreciate that conventional nomenclature fails to give more than an inadequate picture, and it is necessary as well to discuss the relationships in some detail. To facilitate the recognition of the species as rearranged they will be discussed under separate headings and I have proposed new common names for each.

F. psilolaemus—The Montane Redwing.

F. psilolaemus comprises the montane populations of Kenya, Uganda and Abyssinia known by Praed & Grant as *F. shelleyi theresae*, *F. s. elgonensis*, *F. afer psilolaemus* and *F. a. ellenbecki*.

All these birds are found in heath and grasslands above 8,000 ft. All have a high proportion of rich chestnut in the wings and differ from other red-winged francolins in having some barring on the tips of the primaries: the underparts are rich buff mottled with chestnut and with some dark brown or black markings: the facial pattern is broken and ill defined. Birds from the Shoa mountains round Addis Ababa (*psilolaemus*) are small with small bills (wing ♂164–174, bill ♂30–34), and have blackish spots on the throat, indistinct black spotting on the upper breast and rather sparse chestnut and blackish patterning on the abdomen. Birds from the Arussi plateau south of the Abyssinian Rift (*ellenbecki*) are slightly larger than *psilolaemus*, darker on the head and back, the lighter markings being greyer: below the spots on the throat and breast are darker and the patterning is stronger and richer in colour. Birds from Mount Kenya and the Aberdares (*theresae*) are large (wing ♂174–191, bill ♂35–38): they have only occasional speckles on the throat but are heavily spotted on the upper breast: they are darker above than Abyssinian birds and the chestnut markings on the abdomen are richer. Birds from Mount Elgon (*elgonensis*) are similar to *theresae* but darker and richer.

F. shelleyi—Shelley's Redwing.

F. shelleyi comprises the forms known by previous authors as *F. s. shelleyi*,

F. s. whytei, *F. afer uluensis*, and *F. a. macarthurii* Van Someren, 1938, but excludes *theresae* and *elgonensis* which were previously ascribed to *shelleyi* (see above).

All the birds included in this assemblage differ from *F. psilolaemus* in having the breast maroon, chestnut and grey, unmarked with black below the necklace and gorget: the remainder of the underparts are patterned all over with black and white, the pattern basically of white spots on a black ground, but the spots frequently merging to form irregular bars. In Kenya and northern Tanganyika birds of this type with rather small bills, white throats, well-defined facial pattern and necklace and rather small patterning on the abdomen are found on hillsides, grassy plateaux, and clearings in montane forest from Mount Kenya southwards to the Crater Highlands and Mount Meru. On Mount Kenya and the Aberdares they are found at lower levels than *F. psilolaemus* keeping below the montane forest. Since they are confined to uplands above 3,000 ft., their distribution is necessarily discontinuous and some divergence is shown by isolated populations, birds of the Loita Plains in south-western Kenya being rather greyer and those of the Chyulu Hills (*macarthurii*) rather darker than birds from central Kenya (*uluensis*).

The most southern representative recorded of this small-billed form is from Mbulu at 4,900 feet in the highlands south of Lake Manyara in northern Tanganyika. Fifty miles south-east at Salanga on the Bereku Ridge at about 5,500 feet a large-billed bird has been collected which has larger, more open, patterning on the abdomen: between the two localities there is lower, rather open country probably unsuitable to these francolins. Birds of the large-billed type are found on the Uganda/Tanganyika borders and at scattered localities through western and southern Tanganyika, Mozambique, southern Nyasaland, southern Northern Rhodesia, Southern Rhodesia the Transvaal and Natal. The small-billed, small-patterned form of Kenya (*uluensis*) and the large-billed, large patterned form of Tanganyika (*shelleyi*) have been regarded as belonging to different species and the proximity of the two in the Mbulu area lends weight to this view. Nevertheless, they seem to have similar ecological requirements and field habits; and, while in the Mbulu area the topography of the country may inhibit interbreeding, there is a bird from Amani, 200 miles to the west, which is intermediate between the two forms in the patterning on the abdomen, though closer to *shelleyi* in bill size, which suggests there may be no intrinsic barrier.

The long-billed *shelleyi* is found in varying habitats throughout its range. In southern Nyasaland, as in northern Tanganyika, it may be found on montane grassland up to 7,000 feet, but it is also found in Nyasaland and Northern Rhodesia in grass under brachystegia or even mopane at low altitudes, though it is nowhere common. In Southern Rhodesia it is common in Mashonaland and the Midlands, in open grass of the plateau, but scarcer westwards in Matabeleland (Smithers *et al.*, 1957: 46). It occurs at least as far south as Pretoria and Legogot, in the Barberton district of the Transvaal, in presumably the same type of country as in Southern Rhodesia, but in Natal is found in acacia country below 2,000 ft. along the foothills of the Drakensburg.

In northern Nyasaland, the south-eastern Congo and northern Northern Rhodesia the species (as proposed) is represented by another long-billed form (like *shelleyi*), but

with a small patterning (like *uluensis*) and which differs from both in having a buff throat with the facial pattern and necklace freckled and indistinct. This form (*whytei*), like *shelleyi*, is found at varying altitudes and in both brachystegia and montane grassland and, though there is no ecological barrier between them and they have been collected from within 40 miles of each other at Lundazi and Mzimba, no intermediates are known (Benson, 1951: 79). Benson tells me that he believes this is more likely to be due to lack of collecting and to the scarcity of both forms, rather than to the existence of any barrier to interbreeding. The situation may be found to be comparable to that between *uluensis* and *shelleyi* in northern Tanganyika but further research is required.

F. africanus (*F. afer*)—the Greywing.

I regard the South African Greywing as a monotypic species, and do not associate any of the northern short-billed forms with it. It differs from *F. shelleyi* in having a white throat flecked with black, the facial pattern obscured by black-and-white freckling, the patterning on the underparts very small, and the rufous in the wing very much reduced. The bill is small as in *uluensis*. It is found in the grasslands of the mountains of the southern Transvaal, Orange Free State and Cape Province, reaching Natal on the high spurs of the Drakensburg. McLachland & Liversidge (1957: 94) show an overlap in the ranges of *F. shelleyi* and *F. africanus* in the southern Transvaal but I cannot substantiate this, the most northerly specimens of *africanus* recorded being from Potchefstrom and Wakkerstrom, 100 miles south of *shelleyi* at Pretoria, and in rather different country.

In Natal Vincent tells me there is a clear altitudinal distinction between them, *africanus* being found above 6,000 ft. and *shelleyi* below 2,000 ft., while the intermediate levels are occupied by a third member of the group, *F. levaillantii*. Furthermore *F. shelleyi* has an earlier breeding season than the other two species, which would contribute to segregation.

It will be appreciated therefore that *africanus* has, in many respects, the same relationship to *shelleyi* in the Transvaal as *shelleyi* has to *whytei* in Northern Rhodesia and to *uluensis* in Tanganyika, in that it appears to be completely allopatric and to exhibit distinct morphological differences. But, whereas there appear to be no ecological barriers between *shelleyi/uluensis* and *shelleyi/whytei* and the morphological differences are slight, there is a distinct ecological barrier between *shelleyi* and *africanus* and morphological differences are greater, representing a greater degree of divergence. This to me is just sufficient to warrant giving *africanus* specific rank.

F. levaillantoides (olim *F. gariiepensis*)—Acacia Redwing.

F. levaillantoides comprises all the subspecies of southern Africa usually ascribed to this species and in addition the northern populations known by Praed and Grant as *F. afer stantoni*, *F. a. friedmanni*, *F. a. archeri*, *F. a. lorti* and *F. a. gutturalis*.

It will be seen from the foregoing that I regard the red-winged francolins of the northern and southern acacia steppe as conspecific. They differ from *F. psilolaemus* and from *F. shelleyi* in being paler and less patterned below, lacking on the abdomen

the rich chestnut markings of *psilolaemus* or the black-and-white patterning of *F. shelleyi*, having instead sparse chestnut and blackish flecks or streaks, more common in the northern birds.

In southern Africa they are found in the arid zones from coastal Angola through South West Africa, Bechuanaland, Orange Free State and the Transvaal to the east coast in extreme southern Mozambique, associated, at varying altitudes, with open grassland, hillsides and kopjes, and edges to limestone pans. There are sight records (not included on Map 7) from the Lower Orange River (Winterbottom & Courtenay-Latimer, 1961: 11-12 and *in litt.*). The range of *levaillantoides* overlaps that of *africanus* in the Orange Free State and that of *shelleyi* in the Transvaal. There is little information on their relationship here (perhaps because their numbers have been heavily reduced since the country was settled) but it can be expected that *levaillantoides* would be found at lower altitudes than *africanus*, and in drier areas than *shelleyi*.

In the northern acacia belt the red-winged francolins are found in much the same habitat as southern birds, in sparse grass on rocky hillsides and mountains between about 2,000 and 7,000 feet. In central Abyssinia, where the Acacia Redwing is found in the same areas as the Montane Redwing, it occupies the lower slopes and *F. psilolaemus* the higher (Friedmann, 1930: 112-116).

In northern Abyssinia and Eritrea there is an isolated population (*gutturalis*) found in scrub above 6,000 feet (Smith, 1957: 20). These birds appear to be a link between the acacia species and the Montane Redwing *F. psilolaemus*, for, like the montane bird, they have the facial pattern freckled and ill defined. They also differ from other Acacia Redwings in having the abdomen regularly marked with heavy blackish streaks on the feather centres, though the actual shafts are white, while the flanks are broadly streaked with chestnut. However, in colour and in the distribution of patterning below they seem closer to the Acacia Redwings and are tentatively regarded as conspecific with them.

Otherwise variation in pattern among the Acacia Redwings is slight. All have the facial pattern and necklace well defined, but in birds from southern Angola (*jugularis*) south at least to the Cunene, the black-and-white necklace is enlarged on the breast to a broad gorget. The birds from the Benguela area are exceptionally small, and also rather grey, while Cunene birds are larger and rufous. Throughout both the northern block and other members of the southern blocks there is similar, very marked variation in colour between grey and rufous populations, largely associated with ecology, but there is remarkably little consistent difference between northern and southern birds in spite of the great distance separating them; those from the north have commonly, however, fine dark markings on the abdomen that are usually lacking in those from the south and the abdomens are whiter, less buff. The greyest populations are found in the mountains of eastern (British) Somaliland (*lorti*), in the Kalahari (*kalaharica*—see appendix), and in the Benguela district (as already noted). The most rufous birds are found in the Transvaal and Orange Free State (*levaillantoides*), while in both South West Africa (*pallidior*) and southern Abyssinia and southern Sudan (*archeri*) both rufous and greyish micro-populations are found haphazard (see appendix).

It will be seen that, as far as the northern populations of the red-winged francolins are concerned, the subspecies of the acacia zone could be considered conspecific with *F. shelleyi*, since they are allopatric. However, since in southern Africa *F. levaillantoides* and *F. shelleyi* both occur in the Transvaal, two species must be recognised, and as the northern acacia populations are closer both morphologically and ecologically to the southern acacia birds than to *F. shelleyi*, it seems logical to associate them in the same species.

F. levaillantii—Levaillant's Redwing.

I have made no rearrangement in this species, which is universally recognised as comprising scattered populations from north-western Kenya to the Cape and western Angola and which differs from all other red-winged francolins in having an ochre collar and the sides of face and edges of the throat ochre inside the black-and-white facial pattern. Such populations are found in north-western Kenya, where west of the Rift *F. levaillantii* replaces *F. shelleyi* in grasslands and valleys of the plateaux between 6,000 and 8,000 feet. In Uganda and Ruanda it is found at varying altitudes being common in the lower grasslands west of Lake Victoria (south of Bukobo) and on the plateaux westwards to Lakes Edward and Kivu.

It is absent from most of Tanganyika but reappears on the Njombe and Iringa mountains in the south-west, and on the Nyika Plateau of northern Nyasaland, where it is common above 7,500 feet alongside the rarer *F. shelleyi whytei* (Benson, *in litt.*). Another isolated population is found on the Kibera Plateau in Upemba, southern Congo, at about 6,000 feet (Verheyen, 1953: 256), and scattered populations are found in the grasslands of the Balovale and Mongu districts of north-western Northern Rhodesia westwards through Angola to the Mombolo plateau and the Bailundu highlands. In southern Africa it is found only from the Zoutspansberg southwards through the eastern Transvaal, Natal (between 2,000 and 6,000 feet), Basutoland and the coastal districts of eastern Cape Province, keeping to the moister grasslands and even reed-beds in river valleys. It seems, therefore, in the Transvaal, Natal and Orange Free State, where the four species of Redwing occur, that *F. levaillantii* is associated with the wettest habitat.

The distinctive ochre patterning of the face and throat of *F. levaillantii* has already been noted: it is otherwise most like *F. levaillantoides* but is long-billed and darker and richer in colour, with the black-and-white patterning of the necklace and gorget extending in a complete collar round the hind neck below the ochre collar, and the black-and-white stripes from above the eye, which in *levaillantoides* and *shelleyi* run down the side of the face, in *levaillantii* run behind the head to join at the back. In spite of the wide range and broken distribution there is little variation between the populations but in the populations of southern Africa and of the Nyika plateau these stripes continue down the back of the neck to join the black-and-white collar, while in the western and northern populations the ochre collar is unbroken. The Nyika birds (*crawshayi*) are richer in colour than those of southern Africa (*levaillantii*), with more rufous in the wing, and with more black markings on the abdomen, while the northern birds without the stripe on the hind neck (*kikuyuensis*) are otherwise similar to *crawshayi*.

F. finschi—Finsch's Redwing.

The last of the red-winged species, *F. finschi*, is monotypic. It has a very limited distribution being recorded only from about six localities in western Angola, in a strip about 200 miles long from near Nova Lisboa in the south to Vila Salazar in the north, and again from Brazzaville, in the Congo, 350 miles to the north. On Mount Moco in the Bailundu highlands it was found in the brachystegia woodlands and on the bare upper slopes between 6,500 and 7,000 feet (Hall, 1960a: 408) but the specimen from Vila Salazar (American Museum of Natural History) must have been obtained in very different habitat at not more than 2,000 feet, and at Brazzaville Malbrandt and Maclatchy (1949: 142) found it in grassland with neighbouring woods in which the birds took refuge.

It is possible that the different habitats of *F. finschi* may be partly due to competition with *F. levaillantii*, which occupies grasslands in the southern part of the range, but is not found north of the Mombolo plateau.

F. finschi differs from other red-winged francolins in lacking any black-and-white patterning on the face and neck and having the breast grey: it is closest to *F. levaillantii* in having a long bill and the sides of the face and border of the throat ochre, but in *F. finschi* the ochre is not so extensive on the hind neck: the abdomen is a mixture of buff and pale chestnut.

OTHER VARIATION

Considerable individual variation is to be expected in any birds as intricately patterned as the red-winged francolins and is found in all species. There is some local variation, usually in an increase or reduction of rufous and grey in the plumage, associated with ecology. This, as noted, is particularly marked in *F. levaillantoides*, but since the problems it raises are largely nomenclatorial it is discussed fully in Appendix 2.

EVOLUTION

The complex pattern displayed by the seven species of the Red-winged Group is not easy to interpret but I believe may be partly explained by comparison with a rainfall map (Map 7A). From this it will be seen that the range of *F. levaillantoides* falls largely in the parts where the rainfall is below 20 inches in the year, the range of *F. shelleyi* falls between the 20–40 inch isohyets, the range of *F. levaillantii* falls between the 40–60 inch isohyets, while the range of *F. finschi* coincides remarkably with the only two patches south of the Congo rainbelt where there is over 60 inches in the year. Thus a slight increase or decrease of rainfall may be expected to favour the spread of one species at the expense of others. The discontinuous distribution of all species, and the scarcity of red-winged francolins in so many parts of their range, suggests that the present cannot be regarded as a favourable era for any members. This might be due to competition with other groups, but if so it could be expected that *F. levaillantoides* would be more common in the Kalahari, where there is no competition. From the association of so many members of the group with mountains I believe that a colder era would be more favourable to the group as a whole, and it was in some such era or eras, with fluctuations in rainfall, that

continuity in the ranges of the various species was achieved. Conversely warmer eras could be regarded as least favourable and ones most likely to produce isolated populations in which speciation developed.

Even with this hypothesis as a basis a good many interpretations of the pattern present themselves which are largely dependent on which species one believes are most closely related. The following sequences are put forward tentatively on the premise that plumage pattern is the best guide to relationship. I can offer no explanation of the variation in bill size in terms of evolution and relationship but it is worth noting that in this group it is the species and, in *shelleyi*, the subspecies, associated with the higher rainfall areas that have the long bills. The length may perhaps be correlated with the hardness of the ground in which the birds search for food.

The distinctive patterning on the abdomens of *F. africanus* and *F. shelleyi* suggests that their common ancestor split at an early date from the rest of the group. The present distribution suggests they developed in the south; later spreading north to Kenya in a favourable era; later splitting into two blocks, proto-*africanus* and proto-*shelleyi*; later proto-*shelleyi* splitting into three from which the subspecies *shelleyi*, *whytei* and *uluensis* developed. A favourable era must have followed in which their distribution was continuous over the present range.

The species with relatively unpatterned abdomens may have originated in the north. A warm era could be expected to drive members of this block to the extreme north of the range, and also to high altitudes: it can be postulated that proto-*psilolaemus* developed in such an era to specific status and became adapted to montane conditions: later in a favourable era other members of the northern block spread south and west as far as Angola and the lower Congo. A subsequent unfavourable era isolated first proto-*finschi* in the Angola mountains, then proto-*levaillantii* in the mountains of central Africa, and proto-*levaillantoides* in Abyssinia, Somaliland and Eritrea: in isolation each became adapted to different degrees of humidity: subsequent fluctuations in rainfall allow first proto-*levaillantoides* to spread widely through the continent and then proto-*levaillantii*. The small degree of divergence shown between the isolated populations of both species (with the exceptions of *F. levaillantoides gutturalis* in Eritrea which perhaps was isolated earliest) suggests that these dry and wet cold spells were comparatively recent.

A summary of the evolution postulated is as follows:—

Stage 1. The group widespread in eastern Africa in a cold era.

Stage 2. The group split into a northern and southern block.

Stage 3. The southern block spreads north, at least to Tanganyika, and the northern block south to Kenya (Map 7B).

Stage 4. Warm and unfavourable, both blocks split into two: in the south proto-*africanus* isolated in the mountains of South Africa, proto-*shelleyi* possibly in the mountains of Nyasaland: in the north proto-*psilolaemus* isolated at high altitude, possibly on Mount Kenya or Elgon, and the ancestral stock of the other species isolated in the extreme north.

Stage 5. Favourable. Proto-*shelleyi* spreads, possibly to the limits of its present

range. Members of the northern blocks (with unpatterned abdomens) spread south and west to Angola.

Stage 6. Unfavourable. Proto-*finschi* isolated first in Angola: proto-*levaillantii* isolated next in some mountains of central Africa not occupied by proto-*shelleyi*, while proto-*levaillantoides* is cut off in the north. Each becomes adapted to different requirements of humidity.

Stage 7. In a long cold era favourable to the group as a whole, fluctuations in rainfall and temperature favour each species in turn. In some unusually cold spell proto-*psilolaemus* spreads to cover a large part of Abyssinia and Kenya but is later split into isolated populations in the highest mountains. Proto-*shelleyi* following a favourable era is split into three, from which the subspecies *shelleyi*, *whytei* and *uluensis* develop almost to specific status. An unfavourable spell in the north isolates proto-*gutturalis* in Eritrea from the main body of proto-*levaillantoides*: in a subsequent dry spell (during which the acacia spreads to link the northern and southern belts) proto-*levaillantoides* spreads south to Bechuanaland. In a wet spell proto-*levaillantii* spreads at the expense of *shelleyi* and *levaillantoides*, and proto-*finschi* spreads: where the two come together *finschi* is pushed into the mountains.

Stage 8. The present. Too warm to be favourable to any members of the group, the ranges of all species being discontinuous and the birds uncommon in most areas.

THE RED-TAILED GROUP (MAP 8)

(*F. coqui*, *F. albogularis*, *F. schlegelii*)

RANGE AND CHARACTERS

This is a group of small francolins (wing under 150 mm.) which ranges from Senegal to the Sudan, and from central Kenya west to the central Congo and Angola, and south to the Transvaal and Natal: there is an isolated population in the Rift of Abyssinia. Members of the group are found in woodland, savanna and steppe and, in parts of the range, often on the same ground as other francolins, which suggests that their smaller size may make them non-competitive. The group is formed of three species which are allopatric except in the southern Congo and eastern Angola where isolated populations of *albogularis* are found within the range of *coqui*.

All members of the group have a considerable amount of ochre on the sides of the face, spreading as an ill-defined collar on the hind neck: the crown is plain brown or chestnut, contrasting with the back which has a quail-type pattern (except in the females of *schlegelii* in which the striations and cross bars are reduced to a minimum), varying in colour from grey and black to vinous rufous: in the redder birds the rufous in the tail is conspicuous but in some of the greyer forms is no more than a pinkish wash on the outer feathers: the underparts are variable but all birds have a white or buff throat contrasting with the breast: all have black bills with some yellow at the base and yellow legs: the males have a single spur.

SPECIES AND POTENTIAL SPECIES

F. coqui is the most widespread of the three species which comprise the group. It is found in short grass in brachystegia woodland from southern Uganda and northern Tanganyika, southwards to the Rhodesias and westwards to Brazzaville and the edge of the Angola escarpment, but is absent from mountains and from the drier acacia steppe of Tanganyika. South of the brachystegia belt it is found in the acacia savanna skirting the Kalahari, from northern South West Africa to the Transvaal, and in the coastal districts of Natal. Scattered populations in Kenya, southern Abyssinia and the Harar area are also found in acacia (Benson, 1945: 390) finding it common around Yavello and Mega in "open short-grassed country with scattered low thorn bushes at 4,000-4,500 feet".

In West Africa there is a population in the acacia belt of Senegal, the Upper Volta and northern Nigeria that is isolated by 1,000 miles (and the Lower Guinea forest) from the Brazzaville birds, and by nearly 2,000 miles from the Abyssinian birds. In this area *coqui* is found commonly in cultivations, often alongside *F. bicalcaratus* (Blasdale: unpublished). However, it seems that at Potiskum, 150 miles east of Kano in northern Nigeria, *coqui* is replaced abruptly by *F. clappertoni* which occupies the acacia belt eastwards to Abyssinia (Hollis: unpublished). In Abyssinia *clappertoni* occupies the northern and western areas to the centre of the Rift but is replaced by *coqui* in the Harar area in the east and in the Mega/Yavello area of the south.

In *coqui* the quail-type patterning on the back is very consistent and well defined, though the basic colour, and the colour of the head, vary from grey to brown or rufous in different populations. The sexes differ, the males having the sides of the face and throat ochre or light buff without a black eye-stripe or necklace, the females having the sides of the face similar in colour to the males but the throat whiter and having a black necklace and a black eye-stripe that continues as a black line down the sides of the face. The males also have the breast barred while in the females the barring is replaced or overlaid by a pink or grey wash.

There is little significant geographical variation in birds of the southern part of the range, from Angola, the Congo, central Tanganyika and coastal Kenya south to South Africa (*coqui*). All have grey wings and barred abdomens (though the degree of barring is variable) and females have a pink wash on the breast. In the Abyssinian population (*maharao*) the wings are rufous and both sexes have light narrow barring from breast to abdomen, the females having only a faint wash of pinkish grey over the barring on the breast. The isolated West African population (*spinetorum*) also has rufous wings, but is pale above, washed with pink, and there is no barring on the abdomen in either sex: the breast of male is broadly barred and that of the female plain and pinkish-grey. In Uganda, Kenya and Tanganyika the pattern of variation is confused. East of the Rift in Kenya, south to the Arusha area of Tanganyika, there is a population (*thikae*, Grant & Praed, 1934) known only from a few specimens, which shows some approach to the Abyssinian birds in having rufous wings, light barring, and vestigial barring on the breasts of the females, but with no barring on the abdomens in either sex. From the Rift westwards to the eastern shores of Lake Victoria the birds (*hubbardi*) are similar to both the West

African *spinetorum* and the eastern *thikae* in having plain abdomens but the wings are grey like the southern *coqui*, the breasts of the females are plain and grey, and the whole upperparts are rather dark and grey. Birds from west of Lake Victoria (*ruahdae*) are close to the southern *coqui*, but have the black barring broader and more widely spaced. These birds intergrade with *hubbardi* in the Tabora area.

The second species in the group, *F. albogularis*, has a scattered distribution. There is a population in the Gambia, found mostly on the edges of cultivation, but it is rare (Hopkinson, 1923: 129). Other populations are found on the coastal plain near Accra and in the hinterland of Ghana, eastwards through Nigeria to Garoua in the (French) Cameroons. Field notes on these birds are scarce and somewhat contradictory, Serle (1957: 389) finding them common in "the open savannas and rolling hill country" of Eastern Nigeria, whereas Blasdale tells me that further north he has found them only in thick woodland where there is abundant *Isoberlinia doka*. Most localities from which they have been collected lie within the woodland belt (Map 11, Type 17) but Garoua lies within the acacia savanna belt (Map 11, 20) and the specimen was obtained in "open, sandy, sparsely-treed country" (Good, 1952: 67).

F. albogularis is absent from the woodland and savanna belt north of the Congo forest (where *F. schlegelii* is found) but reappears again 1,500 miles away in the south-eastern Congo on the plateaux of Marungu and Kibara, in the Upemba National Park, on the plains of the Balovale district of Northern Rhodesia, and on the treeless dambos of the Zambezi/Congo watershed in eastern Angola.

Above *F. albogularis* is very like *F. coqui* but the quail-type patterning is less well defined in the females, the shaft streaks and barring being narrower: the wings are more rufous (similar in this respect to the east Kenya population, *thikae*). As in *coqui* the females have a black facial pattern and necklace, but it is ill defined, and the males have none, though they differ from *coqui* in having a white throat contrasting with the ochre cheeks, as in the females. In the rest of the underparts the males of *albogularis* are quite distinct from any form of *coqui* being chestnut on the breast with ochre shaft streaks and rich ochre on the abdomen, lacking any dark barring. The females on the other hand are barred, in greater or lesser degree according to the population, with a faint wash of pink or rufous on the breast, and resemble closely the females of the Abyssinian and east Kenya populations of *coqui*. The population of *albogularis* in which the females are least patterned is in the Gambia (n nominate *albogularis*) the barring being light and restricted to the breast and flanks (though varying individually). In birds from Ghana to the Cameroons (*buckleyi*) the barring is generally heavier, usually with only the centre of the abdomen unpatterned. Birds of both sexes from the populations south of the Congo forest are slightly larger and more richly coloured than those from West Africa and in the females of the south-east Congo (*dewittei*) the barring is heavier but no more extensive than in *buckleyi*: the darkest birds with the most heavily barred females are found in eastern Angola and possibly the Balovale district (*meinertzhageni* White, 1944—see appendix).

The third species of the group, *F. schlegelii*, has been considered by Chapin and Peters to be a subspecies of *F. coqui*. I believe it is distinct enough to warrant

specific status and furthermore is closer in several respects to *F. albogularis*.

It is a rare bird, found scattered through the woodland and savanna belt from the eastern Cameroons to the western Bahr-el-Ghazal. From what Cave tells me it seems to be more consistently a woodland bird than *albogularis* and he has the impression that it is found in rather denser woodland than the sympatric *F. icterorhynchus* of the Vermiculated Group, especially where there is *Isobertinia doka*.

Above *schlegelii* is closer to *albogularis* than *coqui*, though the quail type patterning is much reduced and the sexual dimorphism is more pronounced, the males having broad white shaft streaks but few transverse bars while the females are almost unpatterned: both sexes have a soft vinous wash. Below the male of *schlegelii* is like that of southern races of *coqui*, with ochre sides of the face and throat and narrow black and white barring over the breast and abdomen: the female resembles the male on the head and throat but has the breast grey, patterned with cream triangular marks at the base of the feathers, the flanks sparsely barred, and the centre of the abdomen plain cream.

OTHER VARIATION

In the southern populations of *F. coqui* there is local and ecological variation in size and colour; exceptionally small birds are found in coastal Kenya and Natal; grey, pale birds in Bechuanaland (*vernayi*) and pale, rather pinkish birds in South West Africa (*hoeschianus* Stresemann, 1937): other exceptionally grey birds occur in southern Mozambique (Coguno) and may be expected locally in dry conditions, while pockets of more richly coloured birds are associated with richer vegetation. There is otherwise little variation between birds from Natal and the Transvaal north to coastal Kenya and west to Northern Rhodesia, except in the extreme west: here and in Angola the birds are consistently less rufous and the bars on the underparts are narrower and rather closer together (*angolensis*). Birds from Kasai and western Katanga (*kasaiicus* White, 1945) are similar to *coqui* above and *angolensis* below: they intergrade with *coqui* in the eastern Katanga.

In *F. albogularis* of West Africa individual variation in patterning has already been noted. Serle (1957: 388) also found the general colour individually variable between rufous and grey, though there seems a tendency for the coastal population of Accra to be greyer than inland birds.

Individual variation is also found in *F. schlegelii* especially in the females (see Traylor, 1960b: 86).

EVOLUTION

The most striking features of the pattern presented by the Red-tailed Group are the enormous distances separating the north-western and south-eastern subspecies of both *F. albogularis* and *F. coqui*: also, in *F. coqui*, the complexity of variation in East Africa in contrast to the uniformity of southern birds. I feel confident that the discontinuous range of *F. albogularis* is largely attributable to the presence of *F. schlegelii* in the intervening segment of the same vegetational belt, and suggest that the ancestral stock of the two species once had a continuous distribution in the savanna and woodland encircling the Congo forest. To account for the split into two species I suggest this era was followed by a very dry period in which the forest was divided into a western and eastern block each encircled by woodland and separated by a corridor of acacia linking the northern and southern

acacia belts. It can reasonably be postulated that proto-*albogularis* developed in the belt round the western forest and proto-*schlegelii* in the belt round the eastern forest (Map 8B). When the two forest blocks rejoined with a return of humid conditions and the surrounding belts became one again, the central segment of the belt was occupied by proto-*schlegelii* and the western and southern segments by proto-*albogularis*.

It is more difficult to interpret the pattern of *F. coqui* but a logical sequence can be found which will fit into that postulated for the other species. Proto-*coqui* may have been separated from the ancestral stock of the other two species at a time of spread of montane forest and developed in the east while proto-*albogularis*/*schlegelii* developed in the north. With the retreat of the forest proto-*coqui* spread south and west chiefly in acacia savanna. In an unfavourable spell, either too wet or too dry, proto-*maharao* in Abyssinia was isolated. In the very dry era postulated above, in which there was a corridor of acacia in the central Congo, proto-*coqui* could have spread into the northern acacia savanna belt. Subsequently with a return of humid conditions the northern population would be cut off from the southern by woodland and forest. The southern populations nearest the Equator prove adaptable so that, with the return of woodland and savanna and the indigenous *albogularis* to the southern Congo and Angola, *coqui* competes successfully, occupying the woodlands and *albogularis* the more open grasslands and plateaux.

Meanwhile the isolated northern population diverges from southern birds, developing the distinctive unpatterned abdomen in both sexes, and spreads through the northern acacia belt west to Senegal and east through the Sudan to Kenya and Uganda. Here it encounters both the Abyssinian *maharao* and the southern *coqui*. The characters of the present populations of Kenya (*hubbardi* and *thikae*) and of southern Uganda (*ruahdae*) suggest that some interbreeding took place at some period.

The present appears to be favourable to the Vermiculated Group in the north, at the expense of the Red-tailed Group. In the immediate past it seems that *F. clappertoni* has spread west through the acacia belt in the Sudan, eliminating *coqui* between the Nile Valley and northern Nigeria. In the woodland and savanna belt *F. bicalcaratus* flourishes in the west and *F. icterorhynchus* in the east, and competition with these two may account for the scarcity and discontinuous distribution of *albogularis* and *schlegelii*. However, in West Africa *coqui*, though apparently unable to compete with *clappertoni*, is yet able to live on the same ground as *bicalcaratus* on the southern fringe of the acacia belt. The populations of *coqui* in eastern and southern Africa also seem able to co-exist on the same ground as other francolins.

A summary of the evolution postulated is as follows:—

Stage 1. The group develops in savanna, perhaps in north-eastern Africa.

Stage 2. An unfavourable era, possibly a spread of montane forest. The group splits into two with proto-*coqui* isolated in the east and proto-*albogularis*/*schlegelii* to the north of the forest.

Stage 3. More favourable. Proto-*coqui* spreads south and west in rather dry

savanna, mostly acacia. *Proto-albogularis/schlegelii* spreads in the wetter savanna and woodland encircling the lowland forest of the Congo Basin (Map 8A).

Stage 4. A very dry era. The Congo forest is divided into a western and eastern block, each surrounded by its own woodland and savanna belt, with a corridor of acacia between. *Proto-albogularis* develops in the belt surrounding the western block of forest, *proto-schlegelii* in the belt surrounding the eastern block. *Proto-coqui* spreads through the acacia corridor into the northern acacia belt. In an unfavourable period in the north-east *proto-maharao* becomes isolated (Map 8B).

Stage 5. More humid. The two blocks of forest rejoin and the two savanna belts become one again, the eastern segment being occupied by *proto-schlegelii* and the western and southern segments by *proto-albogularis*. In the southern segment, as woodland and savanna return to districts previously acacia, *proto-coqui* is not pushed out but becomes adapted to woodland and competes successfully with *proto-albogularis* which takes to the more open grasslands. In the north *proto-spinetorum* subsp. spreads west to Senegal and east to Abyssinia and Kenya and diverges from the southern birds. There is limited interbreeding where the northern birds re-encounter other members of the species in the east.

Stage 6. Favourable for the Vermiculated Group, especially in the north. *F. clappertoni* spreads, eliminating *F. coqui* from the acacia belt in the Nile Valley and Sudan westwards to northern Nigeria. In the woodland and savanna belt *F. bicalcaratus* and *F. icterorhynchus* flourish at the expense of *F. albogularis* and *F. schlegelii*. In the south *F. coqui* co-exists more successfully with francolins of other groups.

SPECIES NOT INCLUDED IN ANY GROUP (MAPS 9 & 10)

Francolinus lathamii

F. lathamii is a forest francolin ranging from Sierra Leone to western Uganda and the southern Sudan.

It appears at first sight quite unlike any other African francolin (closer, except in size, to *F. francolinus* of Asia), being, in the male, largely black below with regular white spots, in the female brown with irregular white spots, the throat black and face patterned, the upper parts mottled rufous and brown with some white streaks on the mantle, the bill black, finer than in other francolins. However, comparison of a pair of *lathamii* with a pair of *schlegelii* suggests that *lathamii* may be more closely related to the Red-tailed Group than to any other francolin. It will be seen that the pattern and the colouring on the upper parts are basically the same, though *lathamii*, as would be expected in a forest bird, is darker and more mottled. Below the patterning of the females has some similarity in the irregular, rather triangular shaped spots: while the spotted male of *lathamii* looks very different from the black-and-white barred male of *schlegelii*, this may not be a very significant difference for in odd abdomen feathers of several *lathamii* the spots are less regular and merge as vestigial bars. The chief differences in fact lie in the shape of the bill and the pattern of the face and throat. Furthermore the first plumage of *lathamii* chicks is very similar to the plain vinous mantle of the female *schlegelii*.

While being confident that there are affinities between *lathamii* and *schlegelii* I am not prepared to guess at what period in history proto-*lathamii* became isolated and adapted to forest. The likeness to one particular species in the Red-tailed Group suggests that its isolation could have been subsequent to the emergence of species within the group, the adaptation to such different habitat accelerating divergence. On the other hand *F. schlegelii* is the species of the Red-tailed Group that lives in the thickest woodlands and, if proto-*lathamii* had broken from the ancestral stock of the Red-tailed Group before the three species had diverged, the similarities between *lathamii* and *schlegelii* might be due to convergence. For this reason, and with regard to both its morphological and ecological distinctions, I feel it best to treat *lathamii* independently.

It will be seen that I am not prepared to regard the black-and-white spotting in the males of *lathamii* as indicative of relationship with *F. francolinus*. It has been amply demonstrated in the discussion on groups that the pattern of the underparts is of less significance than size and the pattern above, and while it is interesting that such a striking pattern is repeated in the genus in two such different birds, it cannot be relevant to the grouping of species.

From the distribution plotted on Map 9 it would appear that there is a wide gap between the populations of the eastern and western Congo, but this is more likely to be due to lack of collecting in the central area than to a genuine break. There is little geographical variation, in the males of eastern birds (*schubotzi*) the black-and-white pattern extends further down the abdomen, and the females have the cheeks more rufous than grey, but there is considerable individual variation.

Francolinus nahani

This little francolin is confined to the heaviest forests of the north-eastern Congo and Uganda. It is a distinctive bird, predominantly dark brown or blackish, with white streaks on the underparts and some white spots on the wing-coverts and flanks. The bill is black at the tip and crimson at the base; there is a patch of crimson bare skin round the eye; the legs are crimson, and without spurs in either sex.

It is difficult to assess its affinities with the other francolins. Superficially it appears closest to *F. lathamii* in its small size, general dark coloration and suggestion of spotting, and they occupy the same type of habitat. On the other hand the similarities are in those characters that are to be expected in forest birds, and could well be due to convergence, and the fact that *F. nahani* in the whole of its range is sympatric with *F. lathamii*, without apparently being ecologically segregated, does not suggest close relationship. I would suggest very tentatively that *F. nahani* may have broken off at a remote period from the ancestral stock of the Scaly Group (in the same way as I have suggested that *lathamii* may have broken off from the Red-tailed Group), and become adapted to heavy forest instead of the forest clearings. I suggest this because *nahani*, although much smaller, seems to have some characters in common with the Scaly Group as a whole and with each of the three individual species. In both *nahani* and all species of the group the sexes are alike, and the legs are red: *nahani* is like *F. squamatus* above, having an unpatterned head and

vermiculated back; it is like *F. ahantensis* in the white streaking below; and like *F. griseostriatus* in the crimson base to the bill. Furthermore in all species of the Scaly Group there is a small area of bare skin below and behind the eye, though this is not brightly coloured and usually overlooked.

Chapin considered the absence of spurs to be a generic character and proposed the monotypic genus *Acentrorityx* for *F. nahani*, but the fact that *F. pictus* in India is also without spurs, but yet is so closely related to *F. francolinus* as to hybridise, demonstrates that this character is not necessarily significant. I see no other reason for regarding *F. nahani* as generically distinct.

F. pondicerianus

F. pondicerianus is the smallest of the Asiatic Francolins and is widespread from the shores of the Gulf of Oman eastwards through the plains of India and the dry north-western districts of Ceylon, living in grassland or scrub. It appears to have some affinities with both the Red-tailed and the Striated Groups of Africa and in colour and pattern is closest to *F. coqui*, in particular to the geographically nearest form *F. c. maharao* of Abyssinia. It has "quail-type" plumage on the back, but is duller than *coqui*, with broader transverse white bars and narrower shaft streaks, and with chestnut markings on a grey or buffish ground: the underparts are whitish, irregularly barred with very fine blackish bars: the throat is buff surrounded by a blackish necklace, which is smaller than that found in the females of *coqui* and starts from the chin and not the sides of the bill. In other respects it is closer to the Striated Group (*F. sephaena* and *F. streptophorus*) than to the Red-tailed Group, having a longer and more graduated tail (the tail more than half the length of the wing), and stronger (though not necessarily longer) legs and larger feet, the legs being reddish as in *F. sephaena*. The bill is distinct from either group being brownish in colour and heavier in front of the nostrils. The tail in colour combines characters of both groups being reddish at the base but otherwise largely blackish.

The affinities with two of the African Groups suggest that the ancestral stock of *F. pondicerianus* was isolated from the African stock before the Red-tailed and Striated Groups had diverged and for this reason I have discussed it independently. It seems that, while the African stock underwent many vicissitudes of climate with consequent isolating and regrouping of populations resulting in speciation, the Indian stock had a comparatively tranquil history for in *pondicerianus* there is little variation, and that mostly clinal and ecological: birds from the dry districts of Persia and Baluchistan, east to the western Punjab (*mecranensis*), are the greyest and palest, and those from southern India (*pondicerianus*) the darkest and least grey with the greatest amount of chestnut markings. Those from northern and central India (*interpositus*) are intermediate. Ceylon birds (*ceylonensis* Whistler, 1941) are greyer than either *pondicerianus* or *interpositus* but darker than *mecranensis*.

F. gularis

F. gularis is the swamp francolin of India, being confined to reeds and marshes in the plains of the Ganges, Brahmaputra and their tributaries from central Uttar

Pradesh eastwards into Assam. It is a large francolin, comparable in size and general proportions to the largest member of *F. francolinus*, but with rather a shorter bill and larger feet (as would be expected in a marsh bird). It is, however, quite different in colour and pattern being predominantly a brown and white bird, with a barred back, streaked underparts and a rufous throat, wings and tail. The sexes are alike.

Proto-*gularis* seems likely to have become isolated from other francolins in a dry period and taken refuge in river valleys, becoming adapted to these conditions. The dry era postulated may even have occurred before the link between the Asian and African francolins was broken since the differences from other francolins shown by *F. gularis*, both in ecology and morphology, suggests divergence over a long period.

CONCLUSIONS

THE GROUPS

The chief lesson to be learnt from comparison of the relationships between the members of each group re-emphasises the difficulty of assessing from morphological characters the level of speciation which any form has attained. This is brought home most forcibly by finding that such dissimilar birds as *cranchii* and *afer* in the Bare-throated Group will interbreed freely, while the three Redwings in the Transvaal *shelleyi*, *levaillantoides*, and *levaillantii*, which look more alike, are able, on account of ecological divergence, to live in a small area without interbreeding.

It seems that a relatively slight ecological divergence among the francolins may be effective against interbreeding because their sedentary habits and specialised choice of habitat make them reluctant to move out of their selected type of vegetation. These same habits allow also for comparatively small barriers to act as isolating factors between two populations that are not necessarily ecologically divergent. Two instances have been given where rivers appear to form such a barrier, the Niger between *ahantensis* and *squamatus* of the Scaly Group and the lower Zambezi between *natalensis* and *hildebrandti* of the Vermiculated Group. In the Red-winged Group fifty miles of unsuitable country in Tanganyika between *F. s. shelleyi* at Salanga and *F. s. uluensis* at Mbula serves as barrier to interbreeding between them.

The difficulty of designating in these circumstances which members of groups should be called species and which subspecies was discussed at the start of the paper, for the status of most lies somewhere between the two. This should be borne in mind in the subsequent discussion on evolution, for these "species", which are allopatric members of superspecies, for the most part appear to have attained a level of speciation far below that of those species which are able to live with each other in full sympatry.

EVOLUTION

The stages of evolution postulated for each group have been based on what seem to me to be the simplest and most likely interpretations of the patterns shown, and they represent the minimum number of stages which can be envisaged to produce

such a pattern. They represent a sequence rather than a time-table of change and as such could, in theory, be spread over any number of years. However, there is evidence from the distribution of many montane plants and trees, as well as birds, which shows that there have been periods in which montane forest has spread over vast areas of Africa, linking up the present isolated patches in the Cameroons, Angola, East Africa, Abyssinia, Nyasaland and South Africa, descending as low as 2,000 ft. (see Map 3A). At the same time (by inference a wet era) there would be extensive lowland forest below that level. This would have the effect of reducing the refuges for grassland and woodland species to comparatively small areas isolated from each other by forests. Such conditions would not only be catastrophic for many species but would obliterate any traces of the pattern of distribution and evolution prior to that period. Thus, although such a spread of forest may have occurred during any extensive cold wet era, it follows that, if the stages of evolution I have suggested are accepted, the conclusion cannot be evaded that they have been accomplished since the *last* spread. This conclusion carries with it implications on the rate of speciation which need to be examined closely.

In the course of these stages I have suggested that twelve species of francolins (the ancestral stock of the eight groups and the four independent species) have increased to forty-one, all the new species being members of superspecies. The accompanying dendrogram (Fig. 2) summarises the relationship postulated of the

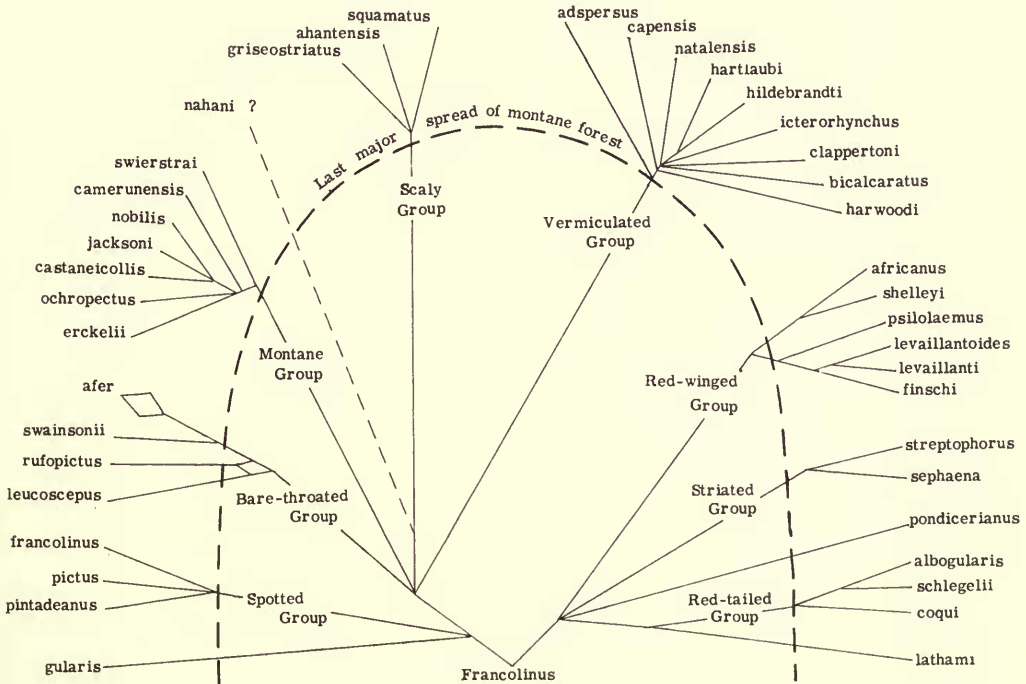


FIG. 2. Dendrogram showing the relationship postulated of the various groups and species, and their date of origin in respect to the last major spread of montane forest.

various groups and species to each other and their date of origin in respect of this last spread. Unfortunately no date can be given yet to this last spread of forest, and there is indeed still uncertainty on the date of onset of the Last Glaciation, opinions varying between 100,000 and 50,000 years ago. Authorities, however, agree that it ended about 18,000 years ago and that there have been at least four glaciations in the course of the Pleistocene. I am suggesting therefore that these changes have taken place in the comparatively short period of the Late Pleistocene (i.e. about the last 100,000 years).

If we accept that *Francolinus* may (among other modern genera of birds) have originated in the Oligocene (approximately forty to thirty million years ago) (Van Tyne & Berger 1959: 6-17) and has taken all the time prior to the last glaciation to divide into twelve species, it seems that I am postulating an incredible acceleration in the rate of increase of species. But this is not so, for, as stated, the concept of periodic spreads of forest over vast areas of Africa is inseparable from the acceptance of a high casualty rate among the non-forest species at that period. If, for instance, the present was followed by a cold, wet era that brought with it a wide spread of forest, it is highly unlikely that any of the less successful non-forest species of tropical Africa would survive (e.g. *rufopictus*, *streptophorus*, *finschii*, *albugularis*, *schlegelii*).

Competition between members of different groups in the limited refuges left would eliminate several of the apparently successful species as well (just as *F. clappertoni* appears to have eliminated *F. coqui* from the Sudan), while members of the same group, forced into unprecedented proximity, would probably interbreed freely. Thus the total number of African species could again be reduced to few (if any) more than the nine which survived the previous forest spread. These would be the ancestors of future groups.

Thus while I believe the number of members in any group may fluctuate widely with successive glacial and inter-glacial eras it seems that any increase in the number of groups and independent species would be very slow and not incompatible with the rate of evolution since the inception of the genus.

It could also be suggested that any further increase is unlikely in this figure, which represents the number of birds which have reached a sufficiently high level of speciation to be able to live sympatrically without interbreeding, for it is evident that only a limited number of such birds can be supported in any given area. In birds like the francolins, in which two species are rarely found actually on the same ground, this limit is governed largely by the number of alternative types of habitat, and the unequal distribution of the groups in tropical Africa gives some reason to suppose that this limit may have been reached.

Disregarding the Montane Group, with its extremely specialised ecology, it will be seen that, apart from a relict population of the Striated Group, only three groups, the Scaly, Vermiculated and Red-tailed, are fully represented in the north-western section (from West Africa to the Sudan and Uganda). There is little overlap between the ranges of these groups and where two do occur together one is thriving at the expense of the other. Furthermore over a vast area it appears that members of the most successful group, the Vermiculated, have totally driven out representatives of

other groups, namely the red-tailed *F. coqui* from Lake Chad to the Nile, and the striated *F. streptophorus* between the Cameroons and Uganda. This north-western section is relatively flat with monotonous vegetation, and no very clear-cut divisions between the vegetation belts: the east and south on the other hand, from Abyssinia to South Africa and Angola, is more mountainous in many parts with more varied vegetation, and here no less than six groups are sympatric or partly sympatric. In this section of Africa I have suggested certain instances in which the range of one group has been restricted by competition with another, but it is also evident that several special may thrive in a small area.

I am not competent to discuss the situation in Asia where the development and status of the francolins must be dependent on those of the numerous other genera of gamebirds which I have not studied, but it seems unlikely that there is much room for an increased number of full species.

In arguing that the members of groups may have developed to the level of members of superspecies within the Late Pleistocene I am conscious that this is postulating a more rapid rate of speciation than is usually accepted, though Rand (1951: 567) has suggested that some of the forest subspecies of West Africa may have evolved in the last 12,000 years, while Moreau (1930) gives examples of Egyptian subspecies which have probably evolved in 5,000 years. However, some weight is added to my argument by the evidence collected by Moreau on the climatic fluctuations that have taken place in this period (Appendix 1), which shows that there has been sufficient variation in both temperature and humidity to bring about the wide redistributions of the montane and lowland forest, woodland, savanna and steppe that would be necessary to the different stages proposed. Furthermore, it shows that all the vegetational changes postulated in the evolutionary sequences in the groups (which were founded entirely on the evidence of the birds alone) did, or could, take place, though it is not always easy to satisfy the sequence.

To support some of the major changes which I have envisaged, he has shown, for instance, that there have been very dry periods prior to 10,000 years ago in Angola and Katanga (at least) which, if they prevailed elsewhere, could have been sufficient to connect the northern and southern acacia belts in the way postulated in the evolutionary sequences of the Bare-throated, Striated and Red-winged Groups. He gives corroboratory evidence for the existence of such a dry corridor at some period in Tanganyika, and Benson and White (in press) suggest this corridor may have been through the Luangwa and Rukwa valleys, and they list many species of birds and mammals whose present distribution has led them to this conclusion.

Moreau shows also that there was a period (undated) at which Lake Chad was 600 miles long, probably with forest at the southern end joining the main Congo forest, so forming a barrier between eastern and western woodland or grassland species, such as was postulated in the Vermiculated Group to split proto-*bicalcaratus* from proto-*icterorhynchus*. He quotes too a record that suggests there was probably lowland forest at Oldowai in northern Tanganyika in the early Pleistocene where there is now acacia steppe. Though this dating can hardly be correlated with the spread of lowland forest envisaged in the later stages of the evolutionary sequence of the Scaly Group, it suggests that such a spread has taken place once and could

therefore be repeated in similar climatic conditions:—perhaps achieved in even one of the recent minor pluvials in East Africa (less than 35,000 years ago).

Similarly he says that late in the Middle Pleistocene there is believed to have been a dry period when the Congo forest was reduced to strips in the east and west (and possibly also on the northern rim) and that there was acacia in the country between. This makes the sequence of evolution postulated for the Red-tailed Group less improbable than it seemed when I first proposed it (before I had seen Moreau's paper), though this sequence remains the most difficult to correlate with known climatic sequences.

Finally, the undated dry period in the Late Pleistocene when the Sahara advanced 300 miles southward may perhaps be correlated with the stage postulated in the Striated Group when dry conditions prevailed on the ridge of higher country between the Cameroons and Uganda on which proto-*streptophorus* may eventually have been isolated.

All the other climatic changes I have postulated in Africa are relatively small and the occurrence of similar changes is unquestionable, though not necessarily in correct sequence. However, some of the dating for these in West Africa is interesting for the most recent humid period in the north-west (5,000–2,000 years ago) may be the time at which *F. bicalcaratus* spread into Morocco up the north-west coast, and if so the Morocco population, which shows only slight divergence, may have been isolated for only 2,000 years. The lack of divergence between the populations of *F. ahantensis* on either side of the present gap in the Upper Guinea forest also gives support to Moreau's evidence that the gap was once further east "probably as late as the Late Pleistocene".

In the Spotted Group of Asia, as in the African groups, it was postulated that the members developed to specific status after the last glaciation. While it is easier here to argue that the same sequence of isolating and rejoining of species was likely to take place in any glaciation it seems unlikely that the simple pattern which remains now could be the product of more than one such sequence.

Finally, lest any of the foregoing should sound dogmatic, it is necessary to end on the same note of caution that was sounded in the introduction. I am fully aware that all the conclusions are based on circumstantial evidence drawn from my interpretations of the picture as we see it today, which are necessarily fallible since so much of the picture is missing. That it has proved possible to construe the known facts into a logical and coherent story gives some verisimilitude to it and so does the evidence that many of the postulated vegetational changes have actually taken place. However, the story remains hypothetical, but further studies of this nature and researches in other branches of science will corroborate or disprove others of the possibilities suggested so that eventually a picture may emerge that approximates to reality.

SUMMARY

1. It is found that the genus *Francolinus* (including *Pternistis*) is comprised of eight groups, the members of which are largely allopatric, and four independent species.

2. Some of the difficulties are discussed of defining the relationship between the members of the groups.
3. The value of different characters as a guide to relationship is illustrated by comparison between the groups.
4. Each group is studied in turn and the characters and ranges of its component members defined. In doing this it was found necessary to review the systematics of the Redwing and Greywing Francolins of the species *africanus* (*olim. afer*), *levaillantoides* (*olim. gariiepensis*) and *shelleyi*.
5. An attempt is made to postulate the sequence of evolutionary stages through which each group has developed, and the climatic and vegetational changes which have accompanied each stage.
6. The four independent species are discussed.
7. Comparison between groups suggests that slight ecological divergence may be an especially effective barrier to interbreeding.
8. It is concluded that most members of groups reflect in their characters, relationship, and present ranges, the climatic changes that took place in the Late Pleistocene, subsequent to the last glaciation, or, in Africa, the last extensive spread of montane forest. Consequently it is suggested that the number of species of this status is liable to fluctuate considerably in glacial and inter-glacial periods, though the number of groups and independent species may remain more or less constant.
9. These conclusions are supported to some extent by evidence provided by R. E. Moreau of climatic changes that have taken place in the Late Pleistocene (Appendix 1), but more evidence is needed from all branches of science to evaluate them fairly.

APPENDIX 1

Summary of some conclusions reached by R. E. Moreau on the climatic fluctuations in Africa as set out in his paper "Vicissitudes of the African Biota in the Late Pleistocene" (in press : to be published in Proceedings Zoological Society, London).

Africa generally (in conformity with world temperatures)

Colder than the present (with associated reduced humidity) in varying degrees for at least 50,000 years prior to 18,000 years ago. In the last extreme phase, extending from about 24,000-18,000 years ago the cooling amounted to about 5°C. Around 7,000-5,000 years ago probably 2°C. warmer, and for some centuries prior to 1500 years ago 1-2°C. cooler, than the present.

Mediterranean Africa and Northern Sahara

A major pluvial period affected at least the western half of the area in the late Middle Pleistocene, prior to perhaps 100,000 years ago. Palaeartic plants and land-

Footnote : Mr. Moreau has very kindly allowed me to include this summary to illustrate my paper but it must be appreciated that most of the conclusions quoted have been qualified in the full text, where reference is given for the authority on which they are based. This summary must not therefore be used as a base for further premises without consulting the full paper. It must be emphasized that the time-correlations of the events referred to in different parts of Africa remain to be worked out.

molluscs advanced some 400 miles southward and persisted in Ahaggar until the Neolithic, some 6,000 years ago.

Between 5,000 and 2,000 years ago it was more humid (at least in the north-west) than at present.

Southern edge of Sahara and sub-Saharan West Africa

The southern edge of the desert has fluctuated in the course of the Late Pleistocene (i.e. about the last 100,000 years) between about 300 miles south and 300 miles north of the present position and these changes probably extended across to the White Nile. Since the Neolithic, i.e. in about the last 5,000 years, a belt of country some 300 miles in width has reverted to desert.

These fluctuations affected the vegetation of coastal West Africa, especially the Upper Guinea forest, and when the desert came south of its present location the area of forest was greatly reduced and further dissected.

At some stage in the Late Pleistocene, not yet dated, Lake Chad increased to an area 600 miles long, extending nearly to Tibesti. This implies a contemporary northward extension (or movement) of the equatorial rain-belt by some 300 miles.

Prior to its capture by the Lower Niger, some 10,000 years ago, the Upper Niger expended itself in large lakes northwest of Timbuktu, in what is now extreme desert.

Congo basin and Angola

Late in mid-Pleistocene very dry, with aeolian re-distribution of Kalahari sand. Congo forest reduced to a strip towards the coast, another along the eastern rim of the basin and perhaps a third along the northern edge. Throughout Late Pleistocene, humid except in Katanga and Eastern Angola. Here arid in the latter part of the Late Pleistocene down to about 10,000 years ago.

East Africa

The "Gamblian" pluvial, with fluctuations in intensity was contemporary with the Last Glaciation and extended down to about 18,000 years ago, and there have been subsequently at least two short periods more humid than the present. Owing to the broken topography the vegetational effects would have been, in the main, local advances and retractions of vegetation types. In Somaliland the fluctuations were minor and the country always to some degree dry. (Note: There is evidence that at some period in the Early Pleistocene lowland forest extended at least to Oldowai in northern Tanganyika. Also at some period in the Late Pleistocene a corridor of acacia probably extended through Tanganyika to Northern Rhodesia).

Rhodesia and southern Africa

During the Late Pleistocene the rainfall fluctuated between about half and one and a half times the present in the Rhodesias and the Transvaal. Kalahari sand was blowing east as far as the Victoria Falls some 12,000-9,000 years ago. The Orange Free State was drier than the present some 40,000 years ago. South West Africa was never better than semi-arid,

APPENDIX 2

Taxonomic notes and synonymy

SPOTTED GROUP

F. francolinus

Five clinal races have been recognised and further sub-division does not seem useful. Therefore *caucasicus* and *sarudyni* are placed in the synonymy of *francolinus*; *festinus* Koelz, 1955 and *bogdanovi* in the synonymy of *henrici*; *parkeriae* Van Tyne & Koelz, 1955 in the synonymy of *asiae*. Also *billypaynei* Meinertzhagen, 1933, which is a name given to an exceptionally dark micro-population from the Lake of Antioch, is included in *francolinus*.

F. pintadeanus

The characters on which *wellsi* was based do not seem constant and it is accordingly regarded as a synonymy of *pintadeanus*.

I accept Delacour's opinion (1951: 10) that *F. boineti* Bourret, 1944 is an aberrant specimen of *F. pintadeanus*.

BARE-THROATED GROUP

F. leucoscepus

The amount of variation exhibited by the whole species is so slight that numerous subdivisions are not practical. Accordingly *holtemullei*, *muhamedenabdullah*, *keniensis*,* *kiliensis*, *tokora*, *oldowai* Van Someren, 1939, are placed in the synonymy of *infuscatus*.

F. swainsonii

Since *Pternistis* has been submerged in *Francolinus*, *P. s. chobiensis* Roberts, 1932, is pre-occupied and *F. s. lundazi* used instead (see Benson & White, 1957: 138).

A record of the occurrence of *F. swainsonii* at Karonga, at the north end of Lake Nyasa (Long, 1961: 25) was based on a misidentification, the specimens being *F. afer* (Benson, *in litt.*).

F. afer

In the block of vermiculated subspecies there is much individual but little geographical variation. Accordingly *punctulata* and *nyanzae* are placed in the synonymy of *cranchii*.

In the black-and-white birds of Angola and South West Africa variation between the northern and southern birds is too slight to warrant recognition, so *palliditectus* White, 1958 (nom. nov. for *cunenensis* Roberts) is placed in the synonymy of *afer*. In South Africa an intermediate population between *castaneiventer* and *notatus* was named *krebsi*, which I place in the synonymy of *castaneiventer*. In eastern Africa the name *humboldtii* was given to a bird from Tete on the Zambezi, a locality lying in the centre of the zone of hybrids between the black-faced *melanogaster* and the white-faced *swynnertoni*: it is here restricted to the unstable population.

If names are required for the hybrids between the vermiculated and black-and-white subspecies it is convenient in Angola to refer those populations which are closest to *cranchii* to *manueli* White, 1945 (synonyms *camabatelae* Meise, 1958, and *mackenziei* White, 1945), and those which are closest to *afer* to *benguellensis* (synonyms *angolensis* Bocage, *angolensis* Roberts, and *chio* Meise, 1958—see Traylor 1960a: 143–146). Similarly in Tanganyika, Nyasaland and the Luangwa valley those populations closest to *intercedens* may be known as *bohmi* (synonym *tornowi* Meise, 1933), and those closest to *melanogaster* may be known as *itigi* (synonym *aylwinae* White, 1947).

With the merging of *Pternistis* in *Francolinus* *F. coqui angolensis* Rothschild, 1902, is antedated by *Pternistes afer* var. *angolensis* Bocage, 1893, and by the laws of homonymy should be renamed. However Bocage's name *angolensis* was given in error to the same bird which he had named *benguellensis* at the head of his article, and the name was forgotten until listed in the synonymy of *Pternistis afer benguellensis* by Bowen (1930: 157). It thus has remained unused as a senior synonym in the primary zoological literature for more than fifty years and must be considered a forgotten name (nomen oblitum). (Int. Code of Zool. Nomen. 1961. Article

* Also pre-occupied by *F. squamatus keniensis* Mearns, 1910.

23b.) Application is being made to the International Commission for it to be placed on the Official Index of Rejected Names.

MONTANE GROUP

F. castaneicollis

It is probable that most of the micro-populations in isolated patches of evergreen forest are slightly distinct, but it is not practical to recognise by name all those that show minor differences: accordingly *vottegi* and *gofanus* are placed in the synonymy of *castaneicollis*, and *pairizii* Toschi, 1958, in the synonymy of *kaffanus*.

F. jacksoni

It has not been established that variation in the amount of white in the underparts is geographical or associated with altitude. Therefore *guræ* is placed in the synonymy of *jacksoni*.

F. nobilis

F. camerunensis ruandæ Van Saceghem, 1942, is placed in the synonymy of *F. n. nobilis*. It is also pre-occupied by *F. coqui ruandæ* Jackson, 1938.

F. swierstrai

F. cruzi Themido, 1935, is placed in the synonymy of *F. swierstrai*.

SCALY GROUP

F. squamatus

Although there is considerable individual variation no significant geographical variation is recognised from the greater part of the range. Accordingly *tetraoninus*, *zappeyi* and *dowashanus* are placed in the synonymy of *schuetti* and *whitei* Schouteden 1954 (*nom. nov.* for *confusa* Schouteden 1954) in the synonymy of *squamatus*.

It is not thought practical to recognise by name any micro-populations isolated on the mountains of the Kenya/Tanganyika border, since the main trend of variation is clinal. Therefore, *kapiensis*, *kemiensis* and *chyuluensis* Van Someren, 1939 are placed in the synonymy of *maranensis*.

VERMICULATED GROUP

F. bicalcaratus

It has been shown that birds become darker and more heavily patterned towards the south-east of the range, but the differences exhibited in this cline do not seem great enough to warrant separating the birds of the extreme south-east from those of the southern (British) Cameroons. Accordingly *molunduensis* Grote, 1949, is synonymised with *ogilviegranti*.

F. icterorhynchus

The clinal variation does not warrant more than a division into two subspecies. Accordingly *griseescens* is placed in the synonymy of *icterorhynchus* and *emini* and *ugandensis* in the synonymy of *dybowskii*. Birds showing a few chestnut feathers on the flanks, the character on which *ugandensis* was founded, occur sporadically in south-eastern Uganda and must be considered aberrant specimens perhaps indicating past hybridisation with *clappertoni*.

F. clappertoni

F. ischadensis is placed in the synonymy of *F. c. clappertoni* (see text).

The clinal variation shown in southern populations does not warrant extensive splitting; accordingly *cavei* Macdonald, 1940, and *testis* are placed respectively in the synonymy of *gedgii* and *sharpii*.

F. hildebrandti

Numerous subdivisions are not practical; accordingly *helleri* is placed in the synonymy of *hildebrandti*, and *grotei* and *lindi* in that of *johnstoni*.

F. natalensis

The name *thamnobium* Clancey, 1953, was proposed to distinguish paler birds inhabiting drier areas from those of wetter habitats in Natal and the Zoutspansberg (*natalensis*), but since this

gives *natalensis* a discontinuous range it is not practical to recognise the differences by name.

F. hartlaubi

ovambensis is considered a synonym of *bradfieldi*.

F. adpersus

kalahari is considered a synonym of *adpersus*.

STRIATED GROUP

F. sephaena

The name *somaliensis* Grant & Praed, 1934, was given to streaked birds from Somaliland and was based on the misapprehension that the type of *spilogaster* was an unstreaked bird (Rand, 1950: 384). As noted in the text I believe *spilogaster* must be used for the hybrid populations from Somaliland to southern Kenya. However, if it is established that there still exists an unmixed population of streaked birds on the coastal plains which is distinct from the southern *rovuma* then the name *somaliensis* is available. Such a population can be assumed to have existed once since it must be regarded as one of the parents of the hybrid *spilogaster* but it may have been integrated into the hybrid population.

Local variations in size, colour and pattern throughout the species do not seem great enough to distinguish by name. Accordingly *zuluensis* is placed in the synonymy of *sephaena*: *thompsoni*, *chobiensis*, *mababiensis* in the synonymy of *zambesiae*: *schoanus*, *ochrogaster* Hartlaub, 1882, *dehutescens*, and *jubaensis* in the synonymy of *grantii*: Peters (1934: 73) shows that *rovuma* antedates *kirkii*.

RED-WINGED GROUP

F. psilolaemus

On the author's own showing *fricki* is regarded as a synonym of *F. p. ellenbecki* (Friedmann, 1930: 113).

F. shelleyi

There is not sufficient variation between the populations of South Africa and Tanganyika to justify the recognition of *trothae* which is regarded as a synonym of *shelleyi*, as is *sequestris* Clancey, 1960.

F. africanus

Praed & Grant have been among the few modern authors who have correctly regarded *Perdix afra* Latham, 1790, as the senior name of the South African Greywing, known by others as *F. africanus* Stephens, 1890. However, since the submersion of *Pternistis* in *Francolinus*, *Perdix afra* Latham is pre-occupied by *Tetrao afer* Muller 1776, the senior name for the bare-throated francolin formerly known as *Pternistis afer*. The Greywing must therefore now be known as *F. africanus*.

Within the range of the species there is slight local variation but it is not great enough for me to recognise any subspecies: *proximus* Clancey, 1957, is therefore placed in the synonymy.

F. levaillantoides

Roberts (1936: 321) shows that *F. levaillantoides* is the original name for this species and *garipeensis* is a synonym.

In this species the haphazard distribution of rufous and grey micro-populations in the southern districts of the Sudan and Abyssinia and in Angola and South West Africa makes it difficult to know how many subspecies can usefully be recognised. I believe it is impractical to attempt to differentiate between these variations if no other differences are shown, and, furthermore, names should not be used for intermediate populations. Accordingly I recognise in the south—

(a) *F. l. levaillantoides*. All districts east and south of the Kalahari, intergrading with *kalaharica* on the fringes of the Kalahari. Richly coloured (even in the greyest specimens) and heavily patterned. Synonyms, *ludwigi* and *garipeensis*.

(b) *F. l. kalaharica* (Roberts) 1932. The Kalahari. Pale and grey, birds from central

districts almost unmarked on the abdomens; birds from the fringes rather darker with more markings on the abdomen. Synonym, *langi* Roberts, 1932. (Although *langi* has line priority over *kalaharica* I use *kalaharica*, as I am entitled to do as first revisor, since the name was given to a very pale, grey bird from the Damara Pan near the centre of the Kalahari, and thus represents the extreme of variation, while *langi* was given to a rather darker bird from Nkate near the eastern border.)

- (c) *F. l. pallidior*. South West Africa. Either rufous or grey but the rufous birds paler in tone than *levaillantoides*, and the grey birds darker and more heavily marked than *kalaharica*. As known at present the population of the Windhuk area is more rufous, and that of the Tsumeb area greyer (approaching *kalaharica*). Synonym *wattii* Macdonald, 1953. (See Macdonald, 1953, for detailed discussion.)
- (d) *F. l. jugularis*. Southern Angola to the Cunene. Differs from all other subspecies in having a broad black-and-white gorget: typical birds from the Benguela area are small and grey but those from the Cunene are larger and more rufous showing an approach to some of the populations of *pallidior*. Synonyms, *cunenensis* Roberts, 1932, *stresemanni* Hoesch & Niethammer, 1940.

In the north—

- (e) *F. l. archeri*. Extreme southern Sudan to the Golis range of western (British) Somaliland. Similar to *F. l. pallidior* in having both rufous and grey populations but in both the abdomens are paler and commonly marked with fine lines. Synonyms *friedmanni* Grant & Praed, 1934, *stantoni* Cave, 1940.
- (f) *F. l. lortii*. Mountains of eastern (British) Somaliland. Very grey, with a very pale abdomen fairly heavily marked with fine lines.
- (g) *F. l. gutturalis*. Northern Abyssinia and Eritrea. Quite distinct (see text). Synonym *eritrea* Zedlitz.

F. levaillantii

A number of names have been given to the birds of the northern and western populations which have no black-and-white stripe down the ochre collar on the hind neck. However, while the few specimens available indicate that there is a tendency for Angola birds to be paler, the difference is trivial and the series otherwise is remarkably uniform. Accordingly *mulemae*, *adolfriederici*, *benguellensis* Neumann, 1908, *clayi* White, 1944, and *momboloensis* White, 1952 (nom. nov. for *benguellensis*) are placed in the synonymy of *kikuyuensis*.

THE RED-TAILED GROUP

F. coqui

In the populations of central and south-eastern African there is considerable individual and local variation in size and colour so that consistent geographical variation is hard to determine. I do not believe it is practical to distinguish from nominate *coqui* the small coastal birds of Kenya since equally small birds are found in Natal, or to distinguish the populations of Natal, Zululand and southern Mozambique, which on the whole are less rufous, for individuals can be matched with others elsewhere. The names *stuhlmanni* and *campbelli* are therefore placed in the synonymy of *coqui*. I regard *lynesei* Sclater, 1932, also as a synonym of *coqui* since the type is intermediate between *coqui* and *kasaicus* but comes from an area in which the majority of specimens are closest to *coqui*.

For the Uganda race the original spelling "*ruahdae*" has been used since, while the author may have intended the name to be "*ruandae*", there is no clear evidence of this intention in the original publication. (Int. Code of Zool. Nomen. 1961, Article 32a (ii).) *F. coqui ruandae* Jackson, 1938, is accordingly a junior objective synonym. (Article 33a (ii).)

F. albogularis

Serle (1957: 388) shows that *gambagae* must be considered a synonym of *buckleyi*.

The isolated populations of Marungu and Upemba in the south-eastern Congo, the Balovale district of Northern Rhodesia, and of eastern Angola seem to show an increase from east to west in the amount of patterning in the females, and the Angola birds seem also to be darker,

less rufous, than others (Hall, 1960a: 409). Too few specimens are available at present on which to judge the extent of variation, and until there are more, especially of topotypical *meinertzhageni* from Rhodesia, it seems best to use *meinertzhageni* for Rhodesian and Angola birds and *dewittei* for the Congo birds, though I believe that the Rhodesian birds may prove to be closer to those from the Congo than to those from Angola.

F. schlegelii

Traylor (1960: 86) has shown that *confusus* Neumann, 1933, should be considered a synonym of *schlegelii*.

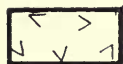
SPECIES NOT INCLUDED IN ANY GROUP

F. pondicerianus

It has been shown that variation in this species is slight and largely clinal and ecological. It is not practical to recognise more than one intermediate subspecies. Accordingly *paganus* Koelz, 1954, *titar* Koelz, 1954, *prepositus* Koelz, 1954, are all placed in the synonymy of *interpositus*.

SPOTTED GROUP—MAP 1

The shaded areas represent the overall ranges of the species. The thick red line indicates divisions between species. The thin red line indicates divisions between subspecies, the zig-zag line denoting intergradation. The red crosses indicate localities from which hybrid specimens have been obtained.



F. francolinus

1. *francolinus*
2. *arabistanicus*
3. *henrici*
4. *asiae*
5. *melanotus*



F. pictus

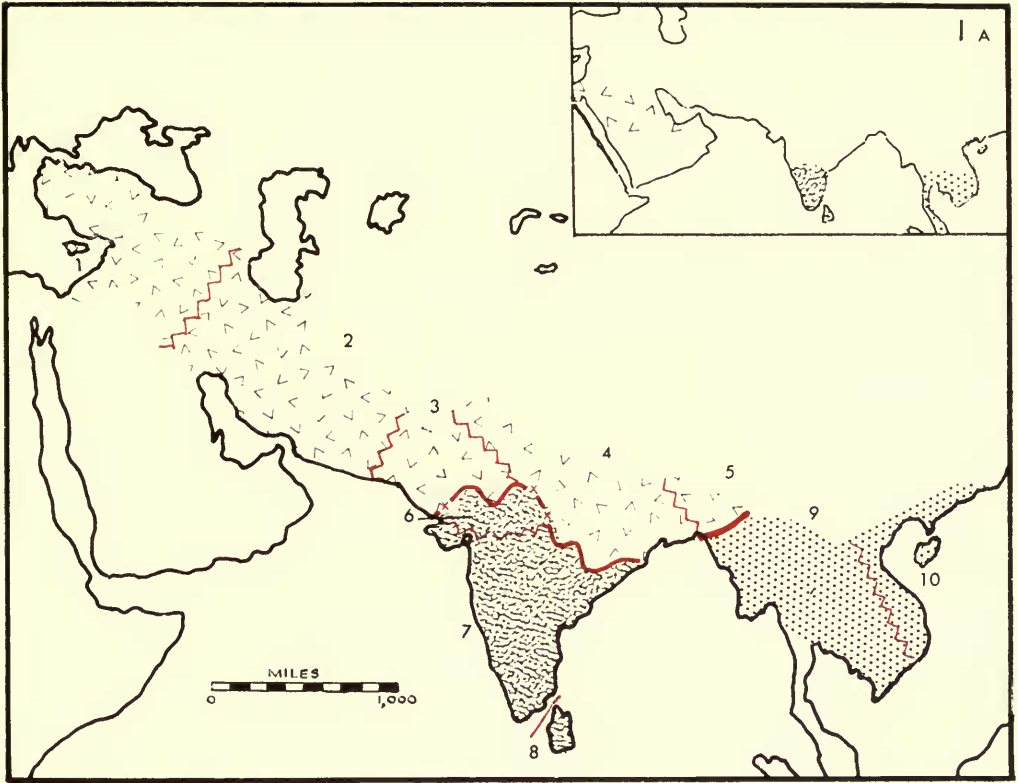
6. *pallidus*
7. *pictus*
8. *watsoni*



F. pintadeanus

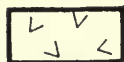
9. *phayrei*
10. *pintadeanus*

MAP. 1A. Hypothetical distribution of the ancestral stock of the three species during a glaciation (Stage 2).



BARE-THROATED GROUP—MAP 2

Overall ranges are shown rather than precise collecting localities. Thick red lines denote specific boundaries. Thin red lines denote subspecific boundaries, plain lines being boundaries between non-intergrading subspecies, zig-zag lines boundaries between intergrading subspecies, toothed lines boundaries of hybrid zones. The red "X" marks the area of hybrids *swainsonii* × *afer*. Numbers have been given only to species and subspecies which are important to the discussion on speciation, but the ranges of other subspecies are indicated.



1. *F. leucoscepus* (*leucoscepus*, *infuscatus*)



2. *F. rufopictus*



3. *F. swainsonii* (*swainsonii*, *lundazi*, *damarensis*, *gilli*)



F. afer. Black-and-white, "afer-type" subspecies

4. *castaneiventer* & *notatus*

5. *lehmanni*

6. *swynnertoni*

6 × 7. hybrids (*humboldtii*)

7. *melanogaster* & *loangwae*

8. *leucoparaeus*

9. *afer*



Vermiculated, "cranchii-type" subspecies

10. *cranchii* & *intercedens*

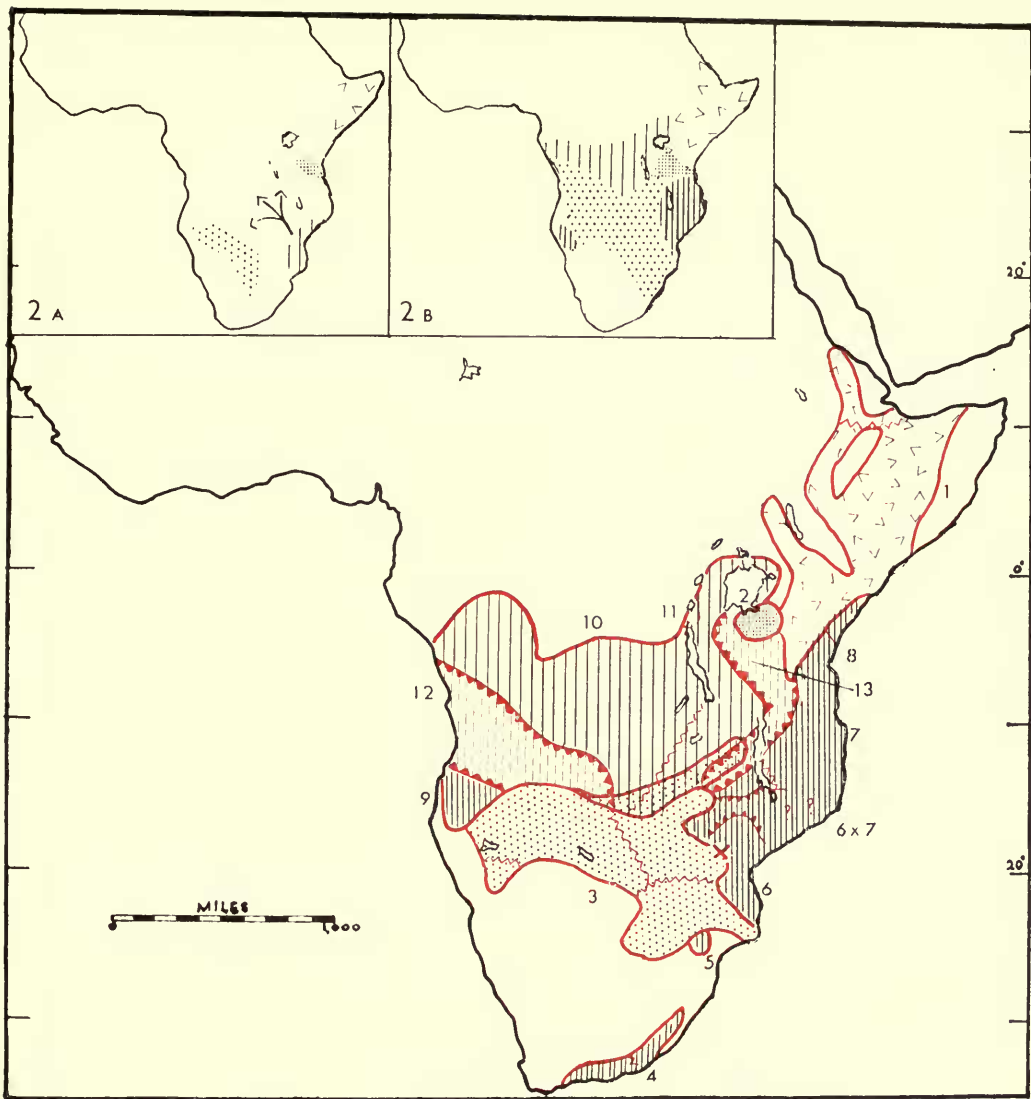
11. *harterti*



Hybrids between "afer-type" and "cranchii-type" subspecies.

MAP 2A. Hypothetical distribution of the ancestral stock of the four species during a spread of forest (Stage 4).

MAP 2B. Hypothetical distribution of the ancestral stock of the four species and two main blocks of *afer* subspecies during a later dry period (Stage 6).

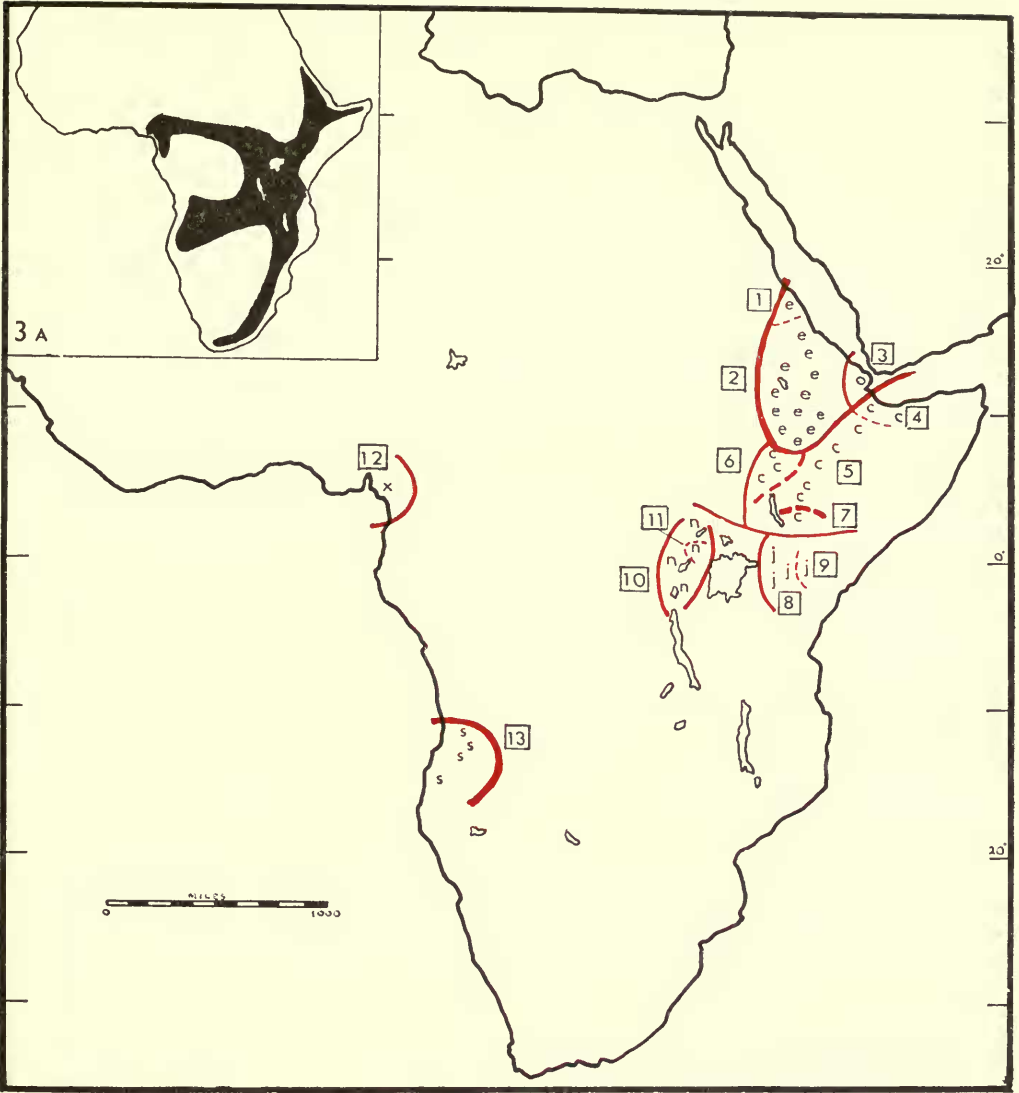


MONTANE GROUP—MAP 3

The letters indicate precise localities from which specimens have been collected. Plain red lines denote divisions between isolates which are regarded as species, and broken lines between those regarded as subspecies. The thickness of the lines is relative to the degree of divergence between neighbouring forms.

e	F. erckelii	1. <i>pentoni</i> 2. <i>erckelii</i>
o	F. ochropectus	3. <i>ochropectus</i>
c	F. castaneicollis	4. <i>ogoensis</i> 5. <i>castaneicollis</i> 6. <i>kaffanus</i> 7. <i>atrifrons</i>
j	F. jacksoni	8. <i>jacksoni</i> 9. <i>pollenorum</i>
n	F. nobilis	10. <i>nobilis</i> 11. <i>chapini</i>
x	F. camerunensis	12. <i>camerunensis</i>
s	F. swierstrai	13. <i>swierstrai</i>

MAP 3A. Hypothetical distribution of montane forest (shaded black) in a cold, wet era (Stage 1).



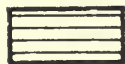
SCALY GROUP—MAP 4

A continuous distribution has been shown for members of the Scaly Group through the Upper and Lower Guinea forests, along the escarpment of Angola, and in the wetter areas of Uganda and Kenya, for within these areas the birds may be expected in suitable clearings or cultivations. Outside this range only general localities from which specimens have been collected have been shaded. Broad red lines indicate divisions between species: thinner red lines denote divisions between subspecies, those that intergrade being indicated by a zig-zag line. Thicknesses of the subspecific lines are relative to the divergence shown by neighbouring forms.



F. *ahantensis*

1. *hopkinsoni*
2. *ahantensis*



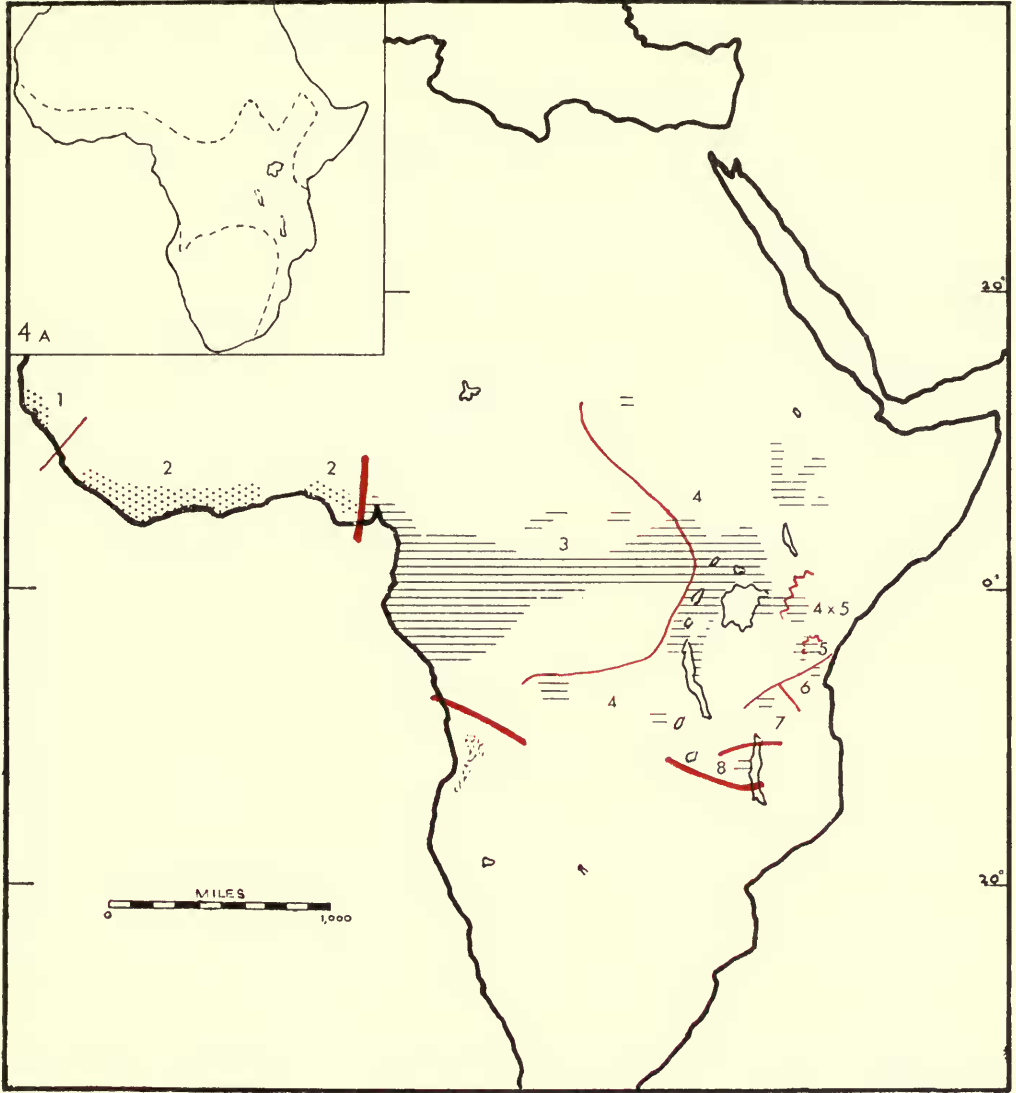
F. *squamatus*

3. *squamatus*
4. *schuetti*
5. *maranensis*
6. *usambarae*
7. *uzungwensis*
8. *doni*



F. *griseostriatus*

MAP 4A. Hypothetical map showing extent of lowland forest in a warm, wet era (Stage 5). Limits of forest shown by broken line.



VERMICULATED GROUP—MAP 5

The distribution of many members of this group is known to be discontinuous. Accordingly only general areas from which specimens have been collected are shaded, but the birds may be expected to occur in some of the intervening areas in which little collecting has been done. Thick red lines denote divisions between species: where there is evidence of hybridisation these lines are toothed. Thin red lines denote divisions between subspecies, those that intergrade being shown with a zig-zag line. The red "X" denotes a hybrid between *hildebrandti* and *natalensis*. The red "T" denotes the aberrant or hybrid specimen *F. tschadensis*. The red "U" denotes the area in which the aberrant "*ugandensis*"-type birds are found.



F. *bicalcaratus*

1. *ayesha*
2. *bicalcaratus*
3. *adamauae*
4. *ogilviegranti*
5. *thornei*



F. *clappertoni*

6. *clappertoni*
7. *gedgii*
8. *heuglini*
9. *sharpii*
10. *konigseggi*
11. *nigrosquamatus*



F. *icterorhynchus*

12. *dybowskii*
13. *icterorhynchus*



F. *hildebrandti*

14. *altumi*
15. *hildebrandti*
16. *johnstoni*



F. *natalensis*

17. *neavei*
18. *natalensis*



F. *hartlaubi*

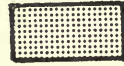
(*hartlaubi*, *bradfieldi*, *crypticus*)



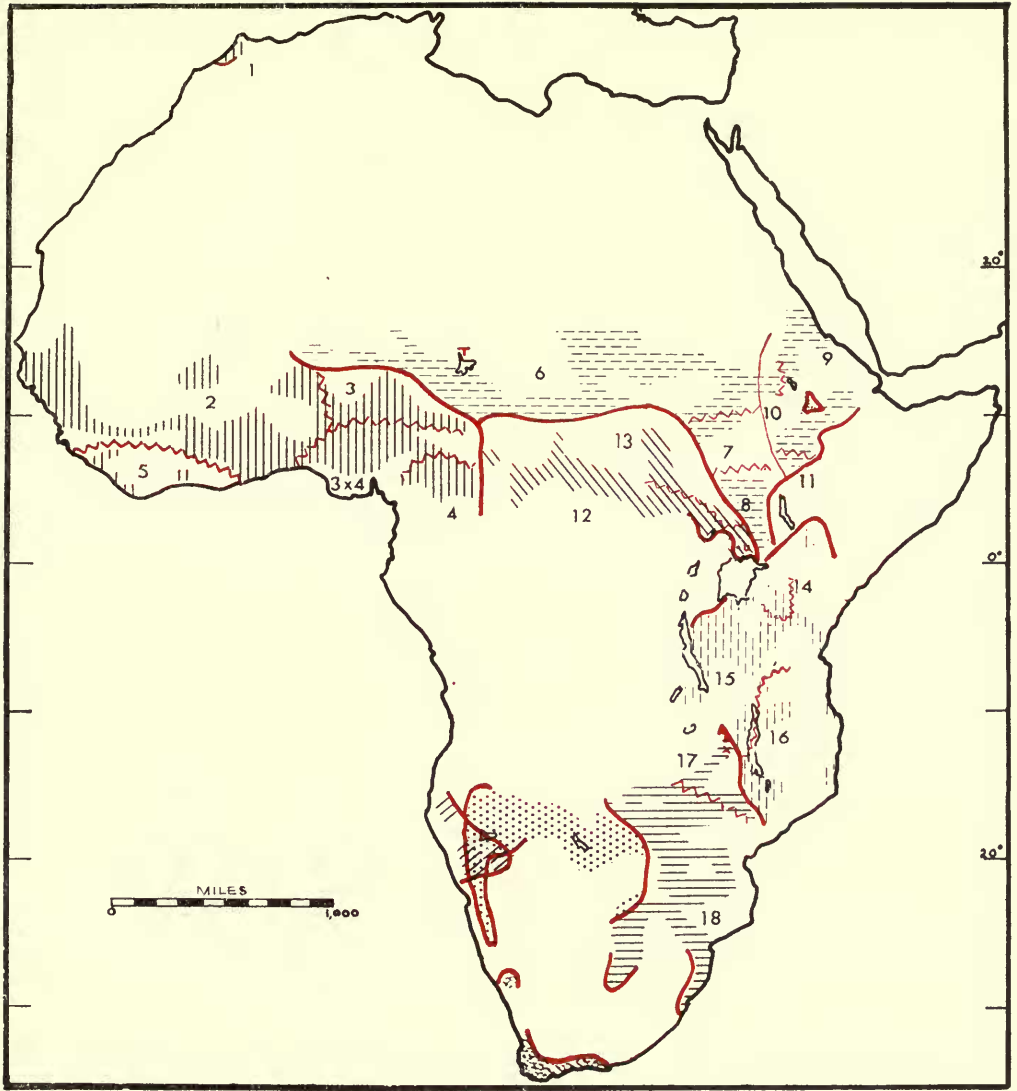
F. *capensis*



F. *adpersus*



F. *harwoodi*

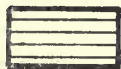


STRIATED GROUP—MAP 6

Only general areas from which birds have been collected are shaded. The broken thick red line indicates the outer limits of the range of *F. streptophorus*, and the unbroken thick red line the outer limits of the range of *F. sephaena*. Thin red lines indicate subspecific divisions, plain lines denoting divisions without intergrading, zig-zag lines denoting intergrading, and toothed lines denoting the boundary of a hybrid area.



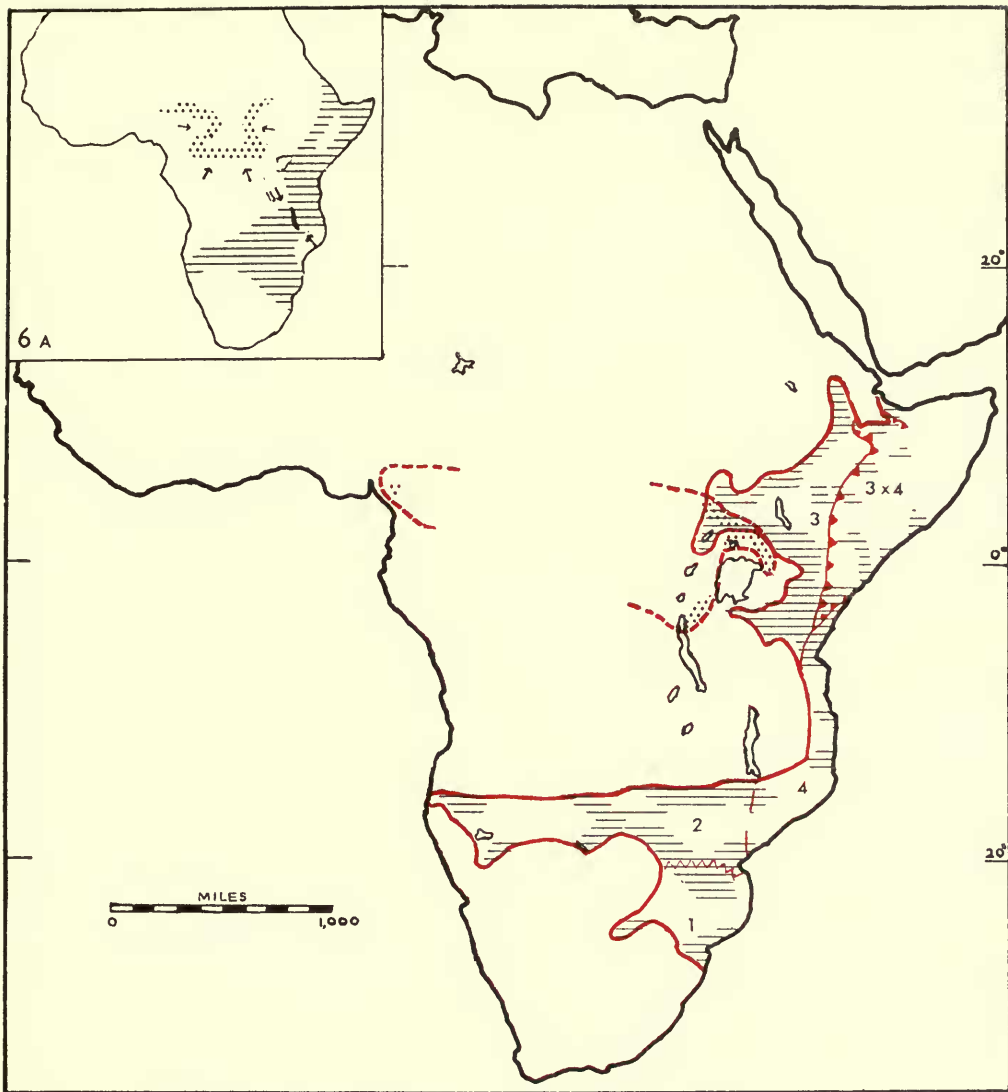
F. *streptophorus*



F. *sephaena*

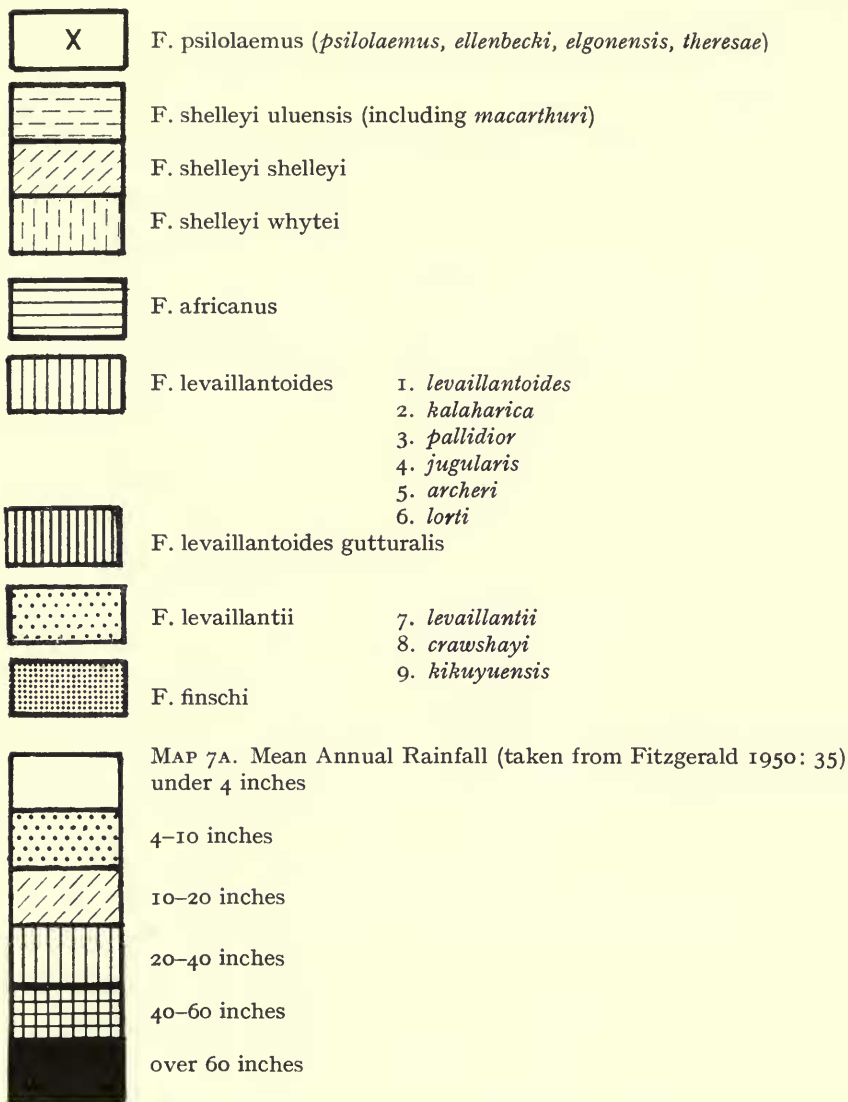
1. *sephaena*
2. *zambesiae*
3. *gratii*
- 3 × 4. *spilogaster*
4. *rovuma*

MAP 6A. Hypothetical distribution of the ancestral stock of the two species at the end of a dry era (Stage 4). Arrows indicate the line of advance of encroaching woodlands.

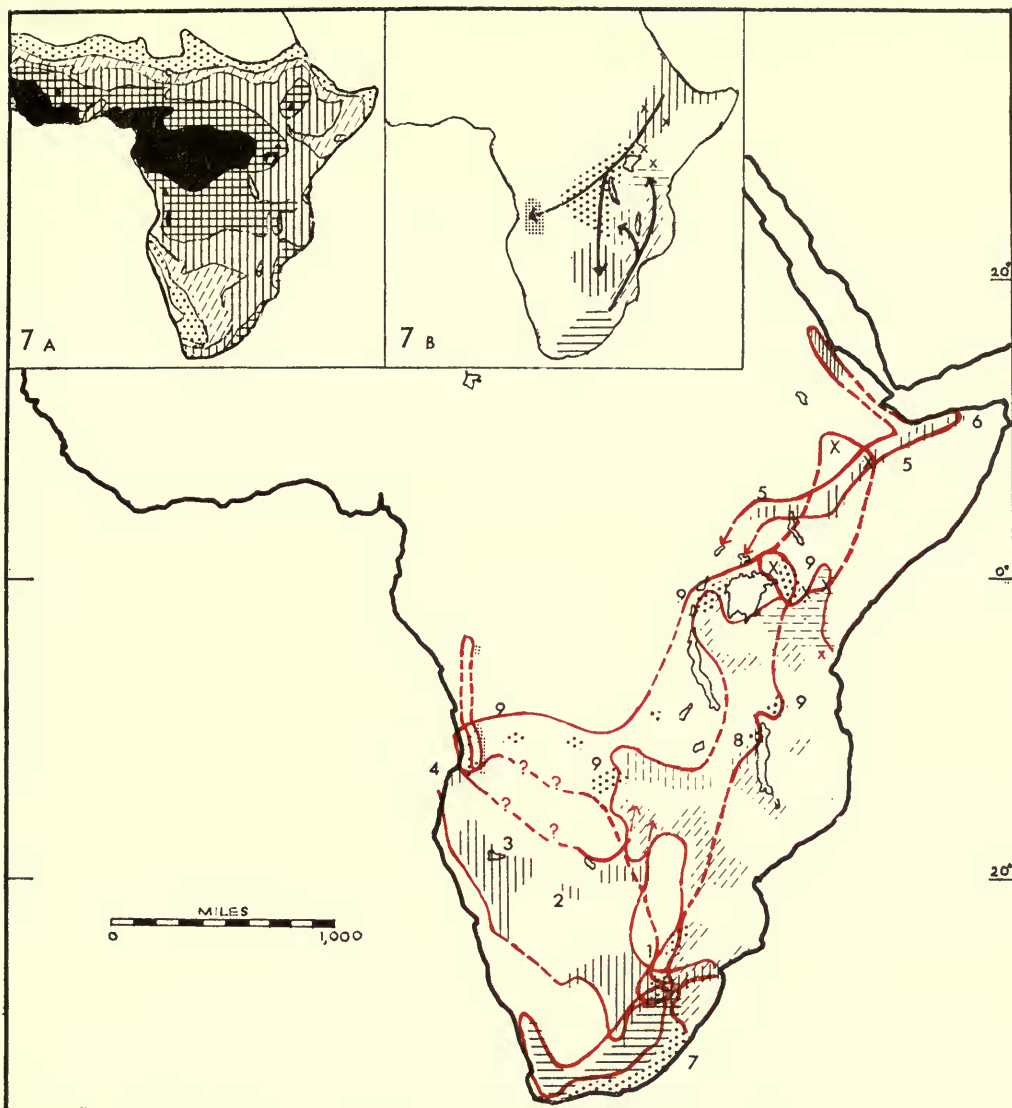


RED-WINGED GROUP—MAP 7

The distribution of all members of this group is discontinuous, accordingly only general areas from which birds have been collected are shaded. Thick red lines denote the extreme limits of the range of each species: these lines are broken where they link remotely isolated populations, except in *F. levaillantoides* where arrows indicate where the lines linking the northern and southern populations might fall. Lineal divisions between subspecies are not shown but different shading has been used for those subspecies which are strongly differentiated: others are numbered. The red cross indicates the Amani specimen which is intermediate between *F. s. shelleyi* and *F. s. uluensis*.



MAP 7B. Diagrammatic map showing hypothetical colonisation routes and centres of speciation (Stages 3–6).



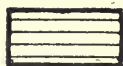
RED-TAILED GROUP—MAP 8

The distribution of all members of this group is discontinuous and only general areas from which specimens have been collected are shaded. Thick red lines denote the extreme limits of the ranges of species, those linking remotely isolated populations being broken, except between the north-western and southern populations of *F. albogularis* where the link is indicated by arrows. Subspecific divisions are shown lineally only in the critical area of Kenya and Tanganyika. Here a toothed line surrounds a population which appears to be a result of hybridisation but which does not now intergrade with neighbouring subspecies: zig-zag lines indicate intergrading. Outside this critical area all subspecies, if not isolates, intergrade.



F. coqui

1. *coqui*
2. *vernayi*
3. *hoeschianus*
4. *angolensis*
5. *kasaicus*
6. *ruahdae*
7. *hubbardi*
8. *thikae*
9. *maharao*
10. *spinetorum*



F. schlegelii

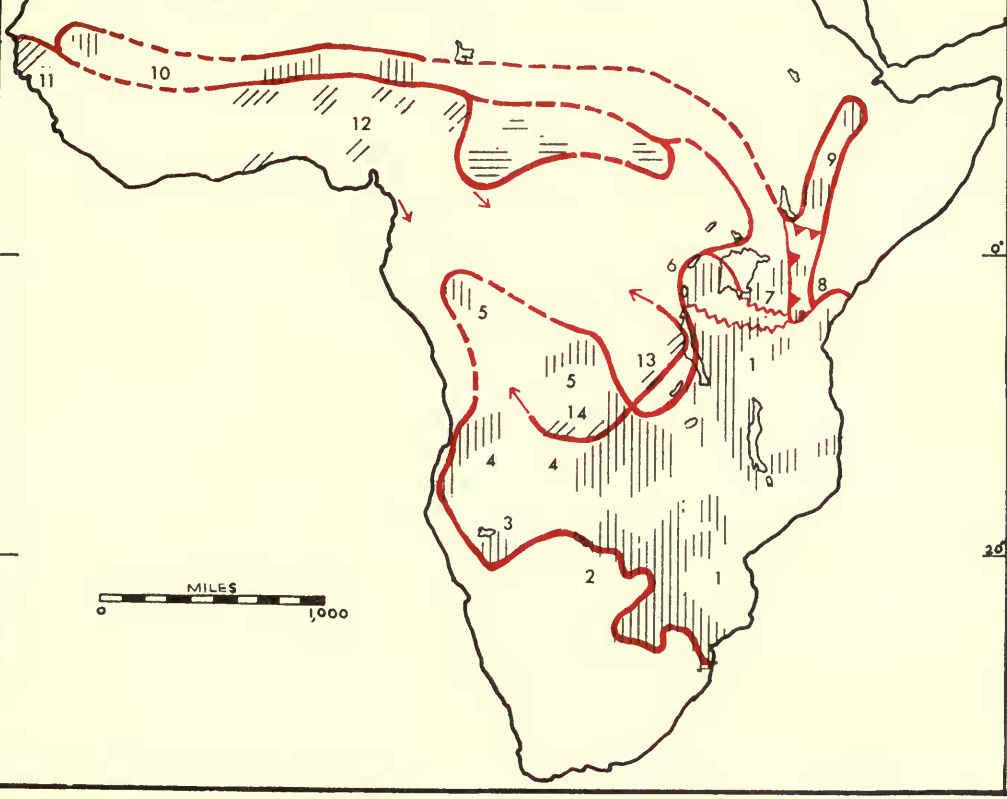
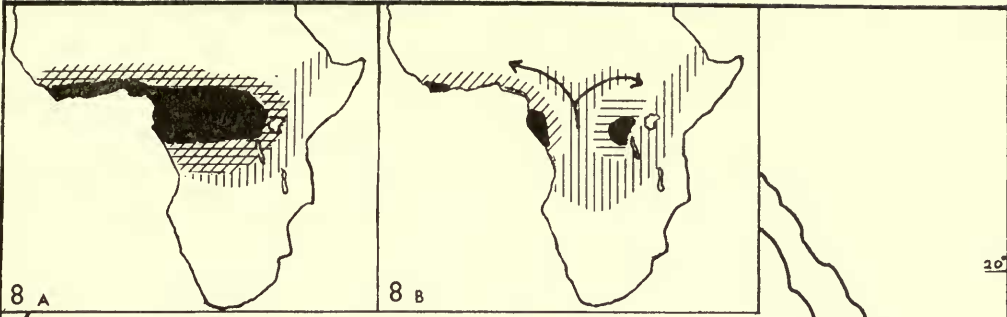


F. albogularis

11. *albogularis*
12. *buckleyi*
13. *dewittei*
14. *meinertzhageni*

MAP 8A. Hypothetical distribution of the ancestral stock of *F. coqui* and proto-*albogularis*/*schlegelii* (shown by mixed diagonal and horizontal shading) before the two latter species diverged (Stage 3). Distribution of lowland forest shown in black.

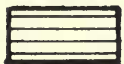
MAP 8B. Hypothetical distribution of the ancestral stock of the three species in a subsequent dry era (Stage 4).



SPECIES NOT INCLUDED IN ANY GROUP
MAP 9



F. nahani



F. lathami

1. *lathami*
2. *schubotzi*



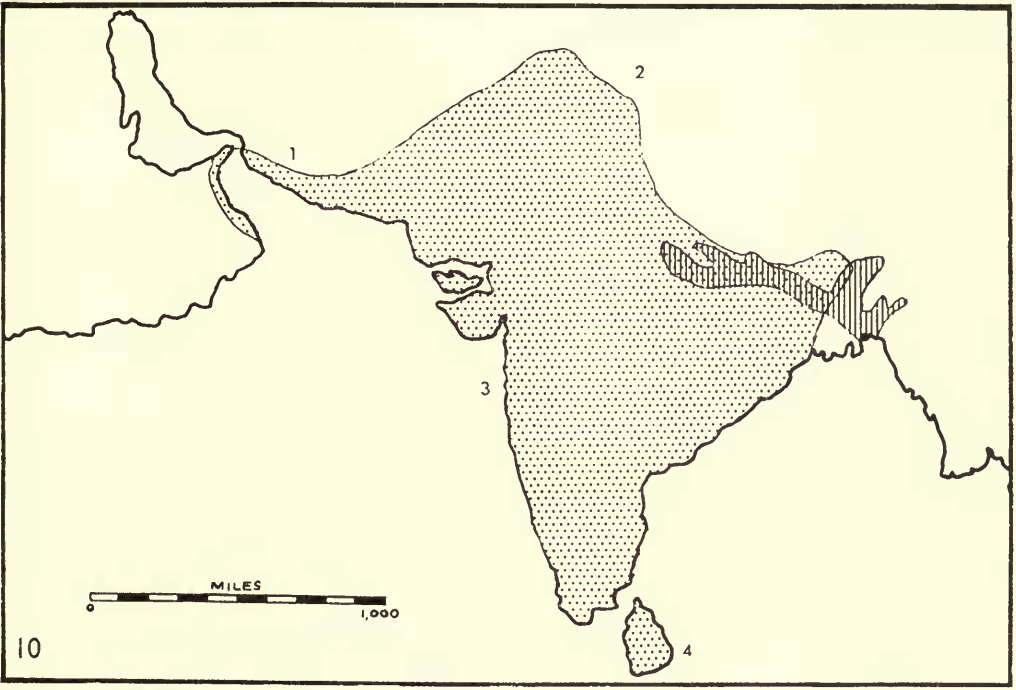
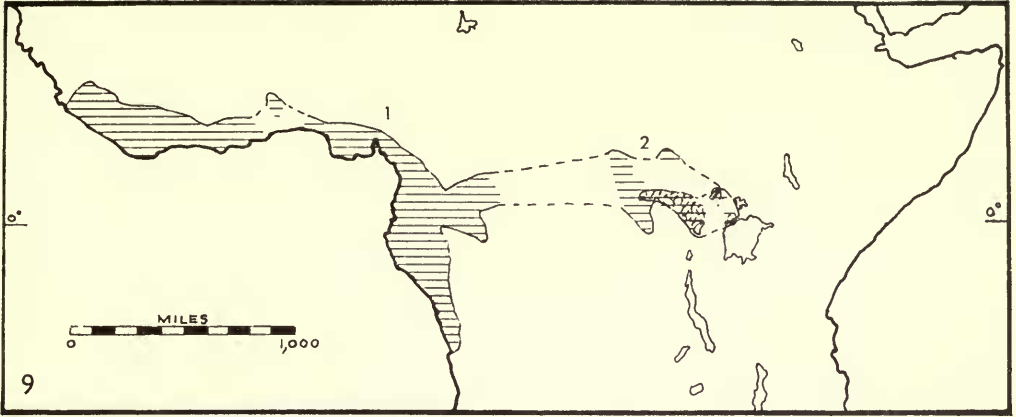
F. pondicerianus



F. gularis

MAP 10

1. *mecranensis*
2. *interpositus*
3. *pondicerianus*
4. *ceylonensis*



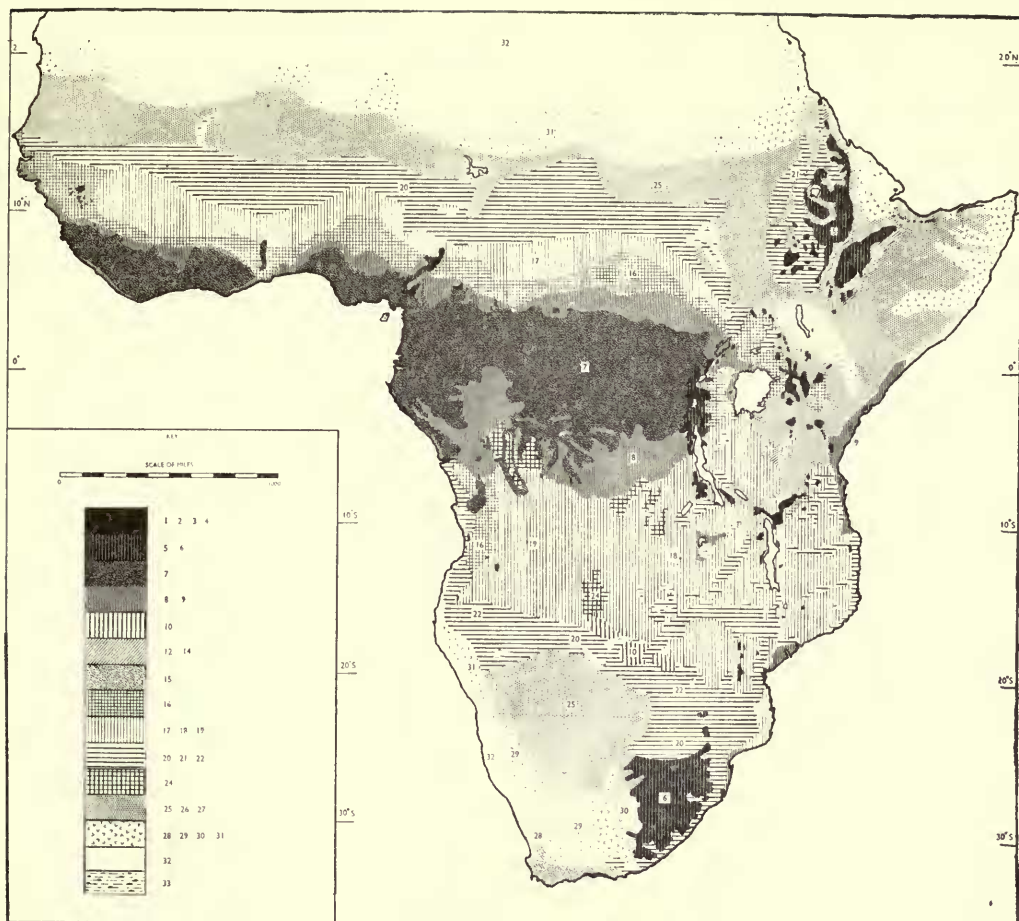
VEGETATION MAP OF AFRICA—MAP 11

Adapted from "Vegetation Map of Africa south of the Tropic of Cancer", Oxford University Press, 1959.

The numbering and terminology of the original map have been used as far as possible, excluding Madagascar. Explanatory notes indicating geographical areas are given in the key in cases where it is not possible to differentiate on the map between vegetation types.

KEY

- 1-4. EVERGREEN FORESTS & MONTANE COMMUNITIES.
1. Montane Evergreen Forest.
 2. Temperate and Subtropical Evergreen Forest. *Knysna and other districts of the extreme south only.*
 3. Montane Communities—undifferentiated. These include evergreen forest (type 1), grassland (type 5) and woodland.
 4. Montane Communities—with afro-alpine communities. *High mountains of central and east Africa and Ethiopia only.*
(It has not been possible on this scale to distinguish between types 1, 3, and 4.)
- 5-6. MONTANE & HIGH ALTITUDE GRASSLAND.
5. Montane Grassland above 6,000 ft. *North-eastern and central Africa.*
 6. Temperate and Subtropical Grassland. *Pure grassland above 3,500 ft. in South Africa.*
7. MOIST FOREST AT LOW AND MEDIUM ALTITUDES.
- 8-9. FOREST-SAVANNA MOSAIC.
8. Moist forest surrounded by savanna of tall grasses. *Found in belts surrounding type 7.*
 9. Coastal Forest-Savanna Mosaic. *East coast only.*
10. DRY & DECIDUOUS FOREST—with abundant *Baikiaea plurijuga*. *Found only in parts of N. & S. Rhodesia, Bechuanaland and the Caprivi Strip, and sometimes regarded as woodland rather than forest.*
- 12 & 14. THICKETS.
12. Itigi type. *Central Tanganyika only.*
 14. Ethiopian evergreen type. *Ethiopia only.*
15. CAPE MACCHIA.
16. RELATIVELY MOIST WOODLANDS. Types in which the genera *Isobерlinia*, *Brachystegia*, and *Julbernardia* are absent or rare.
- 17-19. WOODLANDS (interspersed with Savanna).
17. With abundant *Isobерlinia doka* and *I. dalzielii*. *Northern areas.*
 18. With abundant *Brachystegia* and *Julbernardia*—"myombo". *Tanganyika to central Northern Rhodesia, Southern Rhodesia and Mozambique.*
 19. Similar to type 18 but with a number of distinctive species. Principally on Kalahari sand. *Angola to western N. Rhodesia.*
- 20-22. RELATIVELY DRY WOODLANDS & SAVANNAS.
20. With frequent *Acacia* but other species as well, and savannas of tall grass with certain species of *Acacia*.
 21. Ethiopian types. A heterogeneous assemblage of low deciduous shrubs on stony ground. *Ethiopia only.*
 22. With abundant *Colospermum mopane*. *Southern Africa only.*
24. GRASS STEPPE ON KALAHARI SAND.



25. STEPPES.
 25. Wooded steppe with abundant *Acacia* and *Commiphora*.
 26. Grass steppe with thicket clumps. *Western Uganda only*.
 27. Grass steppe—Luanda type. *Coastal Angola only*.
- 28–31. KAROO & SUBDESERT STEPPE.
 28. Karoo Succulent Steppe. *Western Cape Province only*.
 29. Karoo shrub and grass. *Cape Province and southern South West Africa*.
 30. Transitional and mixed Karoo. *East-central Cape Province*.
 31. Northern areas and northern South West Africa and southern Angola.
32. DESERT.
 33. SWAMPS.

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INDEX TO SPECIFIC AND SUBSPECIFIC NAMES OF *FRANCOLINUS*

Specific and subspecific names of francolins are listed under the nomenclature used in this paper, those of species and subspecies here recognized appearing in roman type, others in italics.

No attention is paid to other generic names that have been given to francolins except in a few cases where the merging of these names in *Francolinus* has created homonyms.

For any species that is here regarded as a member of a species group all the pages of the section dealing with the whole group are listed, regardless of whether the species is actually mentioned on each page.

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